THE INFLUENCE OF HABITAT COMPLEXITY, PREY QUALITY, AND PREDATOR AVOIDANCE ON SEA OTTER RESOURCE SELECTION IN ALASKA

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Abstract

The differential selection of habitat by animals is one of the fundamental relationships that enable species to coexist. Habitat selection may be among various discrete categories (e.g., mudflat, boulder field, or meadow) or among a continuous array of characteristics such as vegetation percent cover, benthic substrate size, substrate rugosity, distance to prey resources, or distance to suitable escape terrain from predation. Sea otters are particularly suitable for resource selection studies because they are capable of selecting a wide variety habitat types in response to prey availability, competition, and predation. In Alaska, sea otters associate with a range of habitats types including continuous bedrock reefs in the western Aleutians to heterogeneous fjord systems in Kackemak Bay, Lower Cook Inlet. Sea otters inhabiting the western Aleutians exhibit highly restricted habitat selection patterns characteristic of declining populations. In contrast, sea otters inhabiting Kachemak Bay exhibit selective use of a broad range of habitat types. Many factors contribute to the selective use of habitats by animals, including habitat suitability, prey quality, and predation risk. This thesis was designed to test factors contributing to sea otter resource selection in an area undergoing population increase versus an area experiencing high predation pressure. The contribution of prey size, abundance, biomass, potential energy density are considered in addition to physical habitat characteristics such as grain size, rugosity, depth, structural habitat complexity, and exposure to prevailing weather. Findings suggest that foraging sea otters differentially select habitat and prey resources based on prey accessibility and not on prey

abundance or potential prey energy density. Findings further suggest that sea otter foraging site selection is based on habitat complexity in areas with increasing populations, but in areas with high predation pressure, proximity to suitable escape terrain appears to be more important than prey quality or benthic habitat complexity.

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This dissertation is dedicated to my late grandmother, Evelyn Stewart, who, through our treasured walks together on the shores of the North Atlantic, instilled in me a passion for exploring marine life.

CHAPTER 1

Introduction

Many factors affect resource selection in animals including population density, competition with other species, food availability and quality, predation, habitat complexity, habitat patch size, and inter-patch distances (Peek 1986, Manly et al. 2002). It is generally assumed that a species will preferentially select resources that are best able to meet its requirements, and that high quality resources will be selected more often than low quality ones (Charnov 1976). Resource selection studies commonly focus on prey or habitat selection.

Prey resource availability and quality is closely associated with predator growth and survival (Oelbermann and Scheu 2002, Rickers et al. 2006). Prey selection may be among various prey species or prey sizes and is affected by factors such as prey abundance, accessibility, handling time, biomass, and energy density (Menge and Lubchenco 1981, Posey and Hines 1991). Prey quality, the relative concentration of energy in prey, can have important implications for predator habitat selection (Mayntz and Toft 2006, Muller-Navarra 2008) as has been shown in cowbirds' selection of grasslands supporting the highest densities of calorie-rich invertebrate prey (Morris and Thompson 1998). Prey quality can vary among habitat patches and within habitat types based on a number of variables, including the relative abundance of chemical constituents in prey (Mayntz and Toft 2006), relative community productivity (Sterner and Elser

2002), and local nutrient dynamics (Branch and Griffiths 1988). Leaf-litter dwelling hexapods, which are important forage for wolf spiders, were found to be nutrient poor when in association with meadow habitats compared to woodland-meadow mosaics (Rickers et al. 2006). Even the selective use of closely related prey species can result in significant differences in predator growth and survival (Toft and Wise 1999) as has been shown in granivorous bird species attaining higher overwintering rates when preferentially feeding on nightshade seeds with higher fat content (Johnson and Robel 1968). Prey quality variation is important because many predators consume a wide range of species. In addition, there is some evidence that individuals of a single prey species can vary in their effects on predator growth rates depending upon the prey's diet (Mayntz and Toft 2006, Malzahn et al. 2007).

Systems that undergo temporal and spatial changes in their productivity can have significant effects on prey selection and predator survival (Folke et al. 2004). Communities that exhibit stable state shifts generally undergo changes in the abundance of key species (Sutherland 1974). Phase states are often characterized by a specific structural and functional species assemblage recognizably different from other assemblages that can occur under the same set of environmental conditions (Holling 1973, May 1977). Although multiple stable states can exist simultaneously, communities typically alternate from one stable state to another as seen in the phase shift from kelp-dominated to urchin barren systems (Steneck et al. 2003). The direct and indirect transfer of nutrients associated with kelp communities (e.g., through herbivory and kelp-detrital food webs) is highly productive compared to the urchin barren state (Harrold and Reed

1985, Gagnon et al. 2004). Although much is known about the consequences of prey distribution and abundance on a predator's foraging efficiency (Toft and Wise 1999, Oelbermann and Scheu 2002), less is known about how variation in prey quality and availability in alternate stable state communities affect a predator's ability to meet daily energy requirements.

The differential selection of habitat by animals is one of the fundamental relationships that enable species to coexist (Rosenzweig 1981). Habitat selection may be among various discrete habitat categories (e.g., mud flat, woodland, or boulder patch) or among a continuous array of habitat characteristics such as vegetation density or percent cover, benthic substrate size, substrate rugosity, distance to prey resources, and distance to suitable escape terrain from predation (Smith 1972, Sih 1980). Consequently, the variables in a resource selection study may be discrete or continuous (Manly et al. 2002). Resources such as habitat are generally not uniformly available in nature and their use may change with availability (Thomas and Taylor 2006). Animals often select habitats based on habitat complexity, prey quality or predation risk (Sih 1987, Lima 1998, Andruskiw et al. 2008). Habitat complexity is an important factor in determining habitat suitability due to its influences on predator foraging efficiency and provision of refuge to prey (Crowley 1978). Predator feeding rate and, ultimately, a predator's ability to meet daily energy requirements is directly influenced by prey accessibility (Menge and Lubchenco 1981). Complex habitats can increase prey survival by decreasing predator foraging efficiency, often through changes in the rate at which predators encounter prey (Smith 1972). Depending on the prey species, optimal refuge from predation may be

obtained by the exploitation of homogeneous fine grain sediments suitable for deep burial (Blundon and Kennedy 1982) or the availability and extent of deep crevices in a continuous bedrock seafloor inaccessible to foraging sea otters (Hines and Pearse 1982).

Sea otters (*Enhydra lutris*) are particularly suitable for resource selection studies because they are capable of selectively foraging in different habitat types, ranging from rocky subtidal reefs to sand or mud-bottom estuaries (Kvitek and Oliver 1992, Estes and Duggins 1995, Laidre and Jameson 2006). In rocky habitats, sea otters select sea urchins and other epibenthic invertebrate prey (Estes and Palmisano 1974) and predation of herbivorous prey generally leads to a kelp-dominated system (Estes and Duggins 1995). In soft bottom substrates, sea otters generally prey on burrowing bivalves and can increase habitat complexity through the excavation of prey (Kvitek and Oliver 1988). Although mixed substrates are common throughout the sea otter range in the north Pacific, little is known about sea otter habitat selection in heterogeneous systems (Kvitek and Oliver 1988, Doroff and DeGange 1994).

The risk of predation can have profound effects on resource selection, foraging efficiency, and the abundance of foraging animals (Sih 1987, Lima 1998). Predators have classically been viewed to directly influence their prey through mortality (Rosenzweig and MacArthur 1963, Taylor 1984). However, predators also have nonlethal effects on their prey thereby influencing activity times, habitat use, and group size (Stein and Magnuson 1976, Sih 1982). Nonlethal effects may result in animals selecting more highly restricted habitats (e.g., shifting activity toward safer but less rewarding food patches) or heightening vigilance at the expense of feeding efficiency (Brown 1999, Lima and Dill

1990, Sih 1980). Intense predation pressure can generate a fundamental trade-off between food and protection, forcing prey species to balance habitat selection between safe and productive locations (Sih 1980, Brown 1999).

Sea otters currently inhabiting the central and western Aleutian Islands exhibit restricted habitat use patterns suspected to be mediated by one of three major hypotheses including killer whale predation (Estes et al. 1998), nutritional limitation, or the need for protection from storms (Kuker and Barrett-Lennard 2010). The possibility that diving marine mammals modify their foraging behavior in response to predation risk has been given little attention despite the consistency among prey behavioral responses to predators (Lima 1998, but see Kramer and Graham 1976, LeBoeuf and Crocker 1996) and the likely importance of non-consumptive predator effects in marine communities (Heithaus et al. 2008, Peckarsky et al. 2008). Recent theoretical models predict that optimal predator dive-foraging decisions under the risk of predation may differ substantially from those of a diver concerned only with energy intake (Heithaus and Frid 2003, Frid et al. 2008). The possibility that sea otter habitat selection could be mediated by predation pressure and that their restricted habitat use is attributable to suitable escape terrain from predation remains to be tested. Nutritional limitation is one explanation for the decline of Steller sea lions (Alverson 1992, Trites and Donnelly 2003) and other marine predators (Österblom et al. 2008) in the North Pacific and Bering Sea based on a shift from energy-rich prey to abundant energy-poor prey (the junkfood hypothesis; Alverson 1992, Rosen and Trites 2000). The degree to which shifts between kelp forests and urchin barrens affect prey quality and whether or not such changes can be attributed

to sea otter restricted habitat use in the central and western Aleutians remains to be evaluated. It has been suggested that sea otter use of sheltered inlets and protected coastlines is driven by the need for protection during storms (Kuker and Barrett-Lennard 2010). Sea otters are known to prefer sheltered areas during rough weather (Kenyon 1969, Rotterman and Simon-Jackson 1988), generally occupying waters <40 m deep and within 400 m from the shoreline (Burn et al. 2003). Given the frequency of storms in the Aleutians, habitats that provide shelter from storms and are prey rich are optimal and therefore expected to be the first areas occupied by expanding sea otter populations and the last areas inhabited by populations that have stabilized at low densities (Kuker and Barrett-Lennard 2010). Whether restricted habitats are being used by sea otters for storm protection remains to be tested.

This thesis was designed to address three research areas regarding sea otter prey and habitat selection in each of the following chapters. Chapter 2 describes patterns in sea otter foraging site selection based on prey composition and habitat type in a heterogeneous estuarine environment to determine if (1) foraging sea otters use rockier and more complex habitats as opposed to finer grain habitats in heterogeneous environments and (2) if sea otter foraging site selection correspond with the availability of larger, more abundant, and higher energy prey. These objectives were achieved by analyzing habitat complexity and prey characteristics at used and unused sea otter foraging sites. Chapter 3 examines prey resources in the alternate stable states of kelp forests and urchin barrens to determine if (1) remnant kelp forests provide greater individual prey biomass than urchin barrens, (2) if kelp forests provide greater prey

energy density per unit area than urchin barrens, and (3) if potential differences in these two communities could affect a foraging sea otter's ability to meet its daily energetic requirements. These objectives were achieved by analyzing sea otter prey abundance, biomass, size and potential energy density and relating these values to the activity budget and metabolic rate of a typical sea otter to calculate the predicted feeding effort in each community type. Chapter 4 examines currently used and historically used sea otter foraging habitats to determine if sea otter restricted habitat use can be attributed to nutritional limitation, predator avoidance, or storm protection. Currently used foraging sites were compared to historically used foraging sites to determine if (1) currently used sea otter foraging habitats provide comparable prey availability and quality to historically used habitats, (2) currently used sea otter foraging habitats provide greater structural complexity (i.e. protection from predators) than historically used habitats, and (3) the location of currently used foraging sites are independent of synoptic storm patterns. These objectives were achieved by analyzing sea otter prey abundance, biomass, potential energy density, habitat structural complexity, and site exposure at currently used and historically used sea otter foraging locations. Chapter 5 briefly discusses general conclusions from this research and recommendations for future research.

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CHAPTER 2

The influence of habitat complexity and prey quality on sea otter resource selection in a heterogeneous environment[1]

Abstract

The sea otters' range consists of mosaics of habitat types. However, sea otter use of heterogeneous environments and their effects on community structure within them are largely unknown. This study examined whether foraging sea otters selectively use habitats based on substrate size and prey availability using a database of foraging activity gathered by VHF tagged otters inhabiting a heterogeneous estuarine system. Selection for substrate type and prey was determined by comparing sites used and not used for foraging. Foraging sea otters used rockier habitats in heterogeneous habitats and use was selective based on ease of access to prey and not on prey abundance, biomass, or potential energy density per unit area.

Key words: habitat complexity, benthic prey, foraging site locations, resource selection.

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[1]STEWART, N. L., KONAR B. and A. M. DOROFF, The influence of habitat complexity and prey quality on sea otter resource selection in a heterogeneous environment, submitted to Marine Mammal Science.

Introduction

Predation is strongly mediated by habitat type in marine systems (Peterson 1979, Menge and Sutherland 1987, Trussel et al. 2006). Complex habitats can increase prey survival by decreasing predator efficiency often through changes in predator–prey encounter rates (Smith 1972, Crowley 1978, Grabowski and Powers 2004). In marine benthic environments, predator efficiency is limited by sediment composition and topographic structure and generally decreases with increasing substrate size and/or reduced sediment penetrability (Micheli 1992). The intensity of predation tends to decrease as prey find refuge in increased structural complexity (Menge and Lubchenco 1981, Johnson 2007). Examples of prey refuges from predation include deep burial in soft sediments (Blundon and Kennedy 1982), burrowing in coarse sediments (Sponaugle and Lawton 1990), exploitation of cracks in rocky substrata (Menge and Lubchenco 1981), and associations with kelp canopy (Watanabe 1984). Substrate size alone can favor one prey assemblage over another; for instance, the survival of the infaunal bivalve *Macoma balthica* was found to be limited by crab predation in muddy sediments (Hines and Comtois 1985), whereas both *M. balthica* and *Mya truncata* survived when loose shell material afforded a refuge from the same predator (Skilleter 1994). Abalones endure intense predation by sea otters through the use of a limited number of inaccessible crevices. Since crevices are a limited resource, surviving abalones persist at low densities (e.g., Hines and Pearse 1982). Thus, both habitat refuge and the adoption of low density

refuge (Lipcius and Hines 1986) can decrease predator efficiency and promote prey persistence.

The differential selection of resources by animals is one of the fundamental relationships that enable species to coexist (Rosenzweig 1981). It is often assumed that a species will select resources that are best able to meet its requirements, and that high quality resources will be selected more than low quality ones (Charnov 1976). Resources such as habitat and food are generally not uniformly available in nature and their use may change as availability changes (Manly et al. 2002). In order to reach valid conclusions about resource selection, the comparison of use and availability is commonly employed (Thomas and Taylor 2006). The use of a resource is defined as the quantity of resources utilized by an animal (or population of animals) in a fixed period of time. The availability of a resource is the quantity accessible to the animal (or population of animals) during the same period of time. Use is said to be selective when resources are used disproportionately to their availability (Johnson 1980).

Sea otters use a number of different habitat types, including rocky reefs, soft bottom estuaries, and fjords. In rocky habitats, otters selectively feed on the largest and most abundant prey first before switching to other smaller, less calorically rich, and less easily captured prey (Ostfeld 1982). High predation rates deplete preferred food sources and the diet of sea otters is subsequently diversified to include a wider variety of less profitable prey species (Estes et al. 1981, Tinker et al. 2008). In general, the rapid removal of large and calorically rich prey like sea urchins in rocky habitats releases kelps from grazing pressure leading to kelp dominated systems (Estes and Palmisano 1974,

Estes and Duggins 1995). In contrast, in soft bottom habitats, sea otters feed on burrowing bivalves and preferentially select foraging areas with smaller and more easily excavated prey rather than adjacent patches containing larger but more deeply buried individuals of the same species (Kvitek et al. 1988). Increased effort required to capture deeply buried prey can decrease the prey value and lead to depth refuges for some infaunal prey species (Kvitek et al. 1992). High predation rates in soft bottom habitats commonly result in decreases in prey abundance and changes in the size structure of prey populations rather than in changes in species diversity (Peterson 1979, Kvitek et al. 1992, Micheli 1992). Ecosystem modification in soft sediments is less obvious than in rocky systems. However, indirect effects of sediment disturbance by sea otters and other benthic predators increase seafloor heterogeneity and likely benefit con-specific predators (Woodin 1978, Oliver and Slattery 1985, Kvitek et al. 1992).

Factors contributing to sea otter foraging site selection and subsequent depletion of prey in both rocky (Estes et al. 1978) and soft-bottom habitats (Garshelis et al. 1986) have been well documented. The broad-scale application of these findings across the sea otters range in the North Pacific, however, has been questioned (Foster and Schiel 1988, Carter et al. 2007). In general, there is concern that portrayals of trophic cascades involving sea otters oversimplify benthic community dynamics and overshadow consideration of the effects of other factors such as physical disturbance and substrate type (Schiel and Foster 1986, Foster 1990). Few studies have focused on the effects of substrate type on resource selection among sea otters (Kvitek et al. 1989, Kvitek and Oliver 1992), and only one study, to date, has described prey preference ranking in a

habitat where both sea urchins and infaunal bivalves co-exist (Kvitek et al. 1993). Many sea otter foraging areas consist of heterogeneous habitat types described by patches of both soft and rocky substrates and a gradient of intermediate grain sizes. Heterogeneous benthic environments are capable of supporting prey assemblages associated with both large and fine sediments (Kvitek and Oliver 1992, Kvitek et al. 1992) and differential distributions of many common epifaunal and infaunal prey species. Despite the prevalence of mixed substrate habitats in the sea otters range, their use and the effects of otter predation on community structure within them are largely unknown.

This study describes patterns in sea otter foraging site selection based on substrate size and prey composition in a heterogeneous environment. In regards to generalities in the current sea otter paradigm, two hypotheses were developed: (1) foraging sea otters will use rockier and more complex habitats as opposed to finer grain habitats in heterogeneous environments and (2) sea otter foraging site selection will correspond with the availability of larger, more abundant and higher energy prey. To test these hypotheses, patterns in sea otter foraging site selection were examined in a population of sea otters inhabiting a heterogeneous estuarine system.

Methods

Study Area - This study was conducted in the Kachemak Bay National Estuarine Research Reserve, southcentral Alaska (Fig. 1). The study area was centered on fjord and nearshore island habitats used predominantly by female sea otters. Sea otters occupy this

area year round, but use is highest in the winter when sheltered bays provide protection from storms originating in the Gulf of Alaska (Schneider 1976, Agler et al. 1995, Doroff and Badajos 2009).

Used vs. Unused Study Design – This study used a *Design I* sampling design (Thomas and Taylor 2006), with the study area divided into grid cells that may or may not be used by individuals in the animal population (see Porter and Church 1987). Some habitats were unused by sea otters during the study period and, therefore, resources in available units were partitioned into two sets consisting of used and unused sites. Resource selection was detected and measured by comparing these two sets of resource units (Manly et al. 2002). In this study, used sea otter foraging locations were compared to unused locations in a population of VHF tagged sea otters occupying the study area (n = 44 tagged otters in a population of ca. 3,596 ± 802, Gill et al. 2009). Importantly, the designation of sites as *unused* refers to non-use during the time that sea otters were being visually observed during the VHF monitoring study (sampled weekly from Aug 2007 to Feb 2009) and the concurrent study described in this paper (Jul and Aug, 2008 and 2009).

The location of used sea otter foraging sites was determined using a database of sea otter spatial habitat use and behavioral activity information gathered by VHF tagged sea otters during a concurrent study in Kachemak Bay conducted by the U.S. Fish and Wildlife Service (Doroff and Badajos 2009, Gill et al. 2009). The database cataloged locations of instrumented animals (n = 44) observed during aerial transects flown weekly from Aug 2007 to Feb 2009. The relative accuracy of each location was classified as high

quality ($\leq$0.5 km) or low quality (>0.5 km), and behavior (e.g., foraging, resting, traveling) and location (GPS latitude/longitude) were reported. Observations only occurred during daytime hours and the average interval between locations was 11 days (adverse weather necessitated multiple attempts during each week). Sea otter behavior at the time of relocation varied during the study period; 45% resting or hauled-out, 16% foraging, 15% swimming, 1% other behavior (such as interacting with other sea otters), and 23% unknown activity (Doroff and Badajos 2009). Possible biases could exist in this database given the time constraints on relocations and the use of aerial observations vs. skiff or shore-based focal observations (*see* Bodkin and Udevitz 1999). For the purposes of the study described here, high quality foraging locations (aerial observations made within 0.5 km) were mapped using GIS (ArcView) and overlayed with a 100 m x 100 m raster grid. Grids with foraging activity were designated as "active" (n = 40 grids), and simple random sampling was used to select a subset of 25 active grids. Depths at active locations were measured using a handheld depth sounder, and only those occurring at mean sea otter foraging depths for female otters (approximately 10 m, Bodkin et al. 2004) were selected as used foraging areas for this study (n = 16). Site depth was determined by averaging 15 random depth measurements taken within each grid. All sites (used and available) were sampled (e.g., grain size, rugosity, prey availability and quality) at high or low slack tide and depth was kept constant using a depth adjustment based on mean tidal height for the study area ($\pm$ 2.5 m based on a 5 m tidal range, Doroff and Badajos 2009).

Unused site locations were selected from raster grids containing no records of otter foraging activity during the two-year FWS study. Candidate grids with similar exposure (aspect, distance from shore) and located ≥ 300 m from a particular used site location were designated as candidate "inactive" site pairs for that location. Simple random sampling was used to select two candidate inactive grid cells for each used location (n = 50 based on the 25 active candidates) and were ground-truthed in the field for depth (see above) and slope. Used sites were sampled first in the field enabling the determination of slope (the difference in depth at the start and end of a 20 m transect tape laid perpendicular to the shore) and subsequent selection of similar slope among inactive site candidates. Inactive sites meeting depth and slope requirements (n = 16) were designated as unused site pairs and sampled. A total of 32 sites were sampled (e.g., grain size, rugosity, prey availability and quality) during July 2008 (n = 9 site pairs) and July 2009 (n = 7) (Fig. 1).

Grain Size and Habitat Rugosity - To determine if foraging sea otters used rockier and more complex habitats in heterogeneous environments, it was necessary to compare physical habitat attributes of used and unused sites. Substrate composition was characterized by estimating grain size, and habitat complexity was characterized by measuring habitat rugosity, a proxy for sea floor relief. The correlation between grain size and rugosity was used to determine the association between the two physical habitat characteristics at the scale used in this sampling design. The use of multiple physical habitat variables to describe habitat complexity in benthic systems requires

proof of correlation between variables at the sampling scale being investigated (Beck 2000).

Grain size was recorded on three randomly placed 20 m transects at random intervals (nine per transect, n = 27 per site) and are presented as mean ± 1 SD. Grain size values were binned as mud, sand, gravel, cobble, boulder, or bedrock using a modified Wentworth scale (Table 1). Larger individual grains (e.g., gravel, cobble, and boulder) were measured *in situ* using a 400 mm ruler.

Habitat rugosity was estimated at three random locations on each 20 m transect (n = 9 per site) using a standard rugosity bar and chain (McCormick 1994). The bar and chain method assigns a numerical value to rugosity by measuring the difference between the actual line length between two points, designated by a rigid 1 m bar, and the observed line length between the same two points, determined using a 3 m chain laid out along the irregular seafloor bathymetry. Homogeneous mud flats tend to have rugosity ratios of 1 whereas heterogeneous boulder fields have ratios significantly greater than 1 (McCormick 1994). Rugosity values are presented as mean ± 1 SD for each site (n = 27).

Prey Availability and Energy Density - Sea otter prey species sampled in this study included mussels, crabs, clams, and urchins. Independent estimates of sea otter prey species based on scat analysis and focal observations conducted in 2007 and 2008 confirmed that these prey are present and are consumed by sea otters in Kachemak Bay (Doroff et al. 2009). To determine if sea otters foraged selectively at sites with larger,

more abundant and higher energy prey, the availability of live prey was determined at used and unused sites. In addition to counts and collections of live prey, prey availability was quantified using the "sea otter cracked shell record". Otter cracked shells are characteristically damaged during the feeding process and are discerned from natural mortality and non-otter predation events (e.g., predation from *Enteroctopus dofleini* or *Pycnopodia helianthoides*) by an intact hinge and a single valve missing ca. half of its shell length (Boulding 1984, Ambrose et al. 1988). The otter cracked shell record has been used extensively in sea otter foraging studies to determine prey preference (Kvitek and Oliver 1992), lower size cut-offs for preferred prey (Fukuyama 2000), and the duration of sea otter residency through the comparison of shell size distributions and abundance (Kvitek et al. 1992). In this study, sea otter cracked shells were used to determine recent and historic foraging use (freshly cracked vs. old) and to make size comparisons between previously taken bivalves and the live bivalve prey assemblage. Prey energy density was determined for both the live prey assemblage and the cracked shell record using species-specific conversion factors for mass-to-energy density (Oftedal et al. 2007) and are presented in terms of $kcal \cdot m^{-2}$.

Live sea otter prey species were collected using six randomly placed 0.25 m^2 x 20 cm deep (0.05 m^3) quadrats along the three 20 m transects at each site. Epibenthic prey species (e.g. crabs, urchins, and mussels) were collected by hand prior to excavation of the quadrat using a standard airlift system (methods described by Kvitek and Oliver 1988). The sampling of rockier habitats entailed the sequential removal of boulders before airlift suction dredging and/or, in the case of bedrock, hand collection solely. The

relative ease of access to prey for sea otters is defined as the ability to pick up prey off the benthos versus needing to remove boulders or dig into sediments to access prey. To determine prey community species richness, abundance, and biomass, all prey samples were identified, counted, and weighed (biomass is reported as shell-free wet weight, SFWW). Only prey size classes used by sea otters were analyzed for abundance, biomass, and energy density. All live *Saxidomus gigantea* shell lengths including individuals below the minimal size threshold for sea otter predation (30 mm, Kvitek and Oliver 1988) were included in shell distribution analyses to enable unbiased comparison to the shell record.

Sea otter cracked shells were collected on three 20 m x 2 m (40 m^2) transects at each site. To determine otter cracked shell abundance and species richness, shells were counted and identified to species. Shell lengths were recorded to determine size distributions at each site and the relative time since predation was estimated by the presence or absence of the adductor muscle and classified as freshly cracked or old (e.g., pitted and decomposing).

Data Analysis - Differences in abundance, biomass, and energy density of live prey species between sites and differences in shell size distributions between the live prey assemblage and the shell record were examined using ANOVA with P-values of ≤ 0.05 considered significant. Pairing of sites was not incorporated into analysis of variance given similar outcomes using randomized block design. Multivariate analysis was used to determine if sea otter foraging locations were attributable to habitat complexity and prey

availability and quality (PRIMER-E v.6, Clarke and Warwick 2001, Clarke and Gorley 2006). Data were square root transformed to reduce the dominant contributions of abundant species, and a similarity matrix of all samples was produced using a Bray–Curtis index. The similarity of used and unused sites in terms of live prey abundance, biomass, and energy density per unit area was visualized using multidimensional scaling ordination. Similarity percentages analysis (SIMPER) was used to determine which taxa contributed most to the observed dissimilarity between used and unused sites.

Results

Grain Size - Used sea otter foraging sites consisted of larger grain sizes than unused site pairs in 15 of the 16 pairs sampled (Table 1). Used sites were dominantly cobble (n = 9) and boulder (n = 7), followed by gravel habitats (n = 1). Given the scarcity of larger and more structurally complex grain sizes in the study area, intermediate grain sizes yielded the highest rugosity values of all substrates sampled. None of the 16 used sea otter foraging sites in this study were sand or mud habitats. In contrast, unused sites were dominantly sand (n = 5) and gravel habitats (n = 5), followed by cobble (n = 3) and mud (n = 1). Where used and unused sites shared common grain size bins (e.g. gravel and cobble), mean grain sizes in unused sites were smaller though differences were not significant (used cobble vs. unused cobble, ANOVA, n = 13, $F = 0.49$, $p = 0.8$, used gravel vs. unused gravel, ANOVA, n = 7, $F = 0.14$, $p = 0.7$). Overall, mean grain sizes were significantly larger at used sites (431.9 ± 385.1 mm) than unused sites (116.5 ±

357.5) (ANOVA, n = 32, F = 23.8, p = 0.016). The site pair that did not conform to the pattern in grain size observed between used and unused sites was a cobble (used) and bedrock (unused) site pair located in a steeply sloping inner fjord. The unused bedrock site matched the cobble site in slope and depth but was notably low relief.

Rugosity - Used sea otter foraging sites were significantly more rugose than unused sites in all 16 pairs sampled (ANOVA, n = 32, F = 27.2, p = 0.0002). The mean rugosity values for used habitats was 2.0 ± 0.6 and ranged from 3.1 ± 0.02 (boulder) to 1.2 ± 0.03 (gravel). The mean rugosity for unused sites was 1.2 ± 0.3 and ranged from 2.1 ± 0.3 (bedrock) to 1.0 ± 0.0 (mud). Grain size and rugosity were significantly correlated at the sampling scale used in this study (Pearson correlation, $R^2 = 0.81$, Fig. 2). The removal of the outlying pair, a large grain size (bedrock) having comparable relief to its smaller grain size pair (gravel), strengthened the correlation between grain size and rugosity ($R^2 = 0.95$).

Shell Record - A total of 3785 otter cracked shells were collected during the study representing four species, *Saxidomus gigantea* (82.6 %), *Macoma calcarea* (8.8 %), *Mya truncata* (2.1 %), and *Leukoma staminea* (6.5 %) (from this point forward, having been introduced, species will be referred to by genus name only). Significantly fewer otter cracked shells were found on the seafloor at used sea otter foraging locations (828 shells) than at unused locations (2957 shells). The shell record at both used and unused sites was dominated by *Saxidomus* shells (Table 2); however, otter cracked shells were notably

smaller at used sites (49 ± 25 mm) than at unused sites (75 ± 45 mm). Shells were also more size limited at used sites than at unused sites (indicated by a smaller shell size distribution, Fig. 3). Although the otter cracked shell record at unused sites consisted of larger and more abundant shells, fewer of these shells were freshly cracked (10%, n = 290) compared to used sites (17%, n = 141). In addition, a greater percent of otter cracked shells were old at unused sites (65%, n = 1916) compared to used sites (47%, n = 378). These findings suggest longer-term use of unused habitats (e.g., more abundant shells with a greater percent of old shells) and more recent exploitation of clams in used sites (i.e., a greater percent of freshly cracked shells).

Live Prey - Live prey density was significantly lower at used sites than unused sites (Table 3, ANOVA, n = 32, F = 97.9, p = 0.002). Unused sites provided roughly two times more prey per unit area than used sites, largely due to infaunal clam abundance. *Saxidomus* abundance was four times greater in unused sites than used sites and contributed significantly to the separation in used and unused sites in multivariate analysis (SIMPER, 76%, Figs. 4). Mixed assemblages of *Macoma*, *Mya*, and *Leukoma* co-occurred with *Saxidomus* and were significantly more abundant in unused sites compared to used sites (ANOVA, n = 32, F = 71.4, p = 0.03). In contrast, used sites supported higher abundances of epifaunal prey, primarily due to patchy distributions of the crab *Telmessus cheiragonus*. *Telmessus* abundance did not, however, contribute significantly to the separation in used and unused sites in multivariate analysis (SIMPER, 17%). The urchin, *Strongylocentrotus droebachiensis,* and the mussel, *Mytilus trossulus,*

occurred in used sites but were notably dispersed and generally found individually within interstitial spaces in larger grain sizes. Used boulder and cobble habitats supported low densities of *Cancer oregonensis* and *Oregonia gracilis,* often partially buried or beneath grains. Scuba sampling methods can underestimate the availability of crab species to sea otters because of their tendency to bury and flee with diver disturbance (M.T. Tinker, pers. comm.). Both *Saxidomus* and *Macoma* persisted in low densities in used habitats and generally occurred within the 5 – 10 cm sediment horizon beneath surface deposits of boulders and cobbles, suggesting a potential habitat refuge in larger grain sizes at these sites. Given the low densities observed among all non-*Saxidomus* clams in both unused and used habitats, it is likely that these species have adapted a low density refuge within larger and more productive *Saxidomus* beds. *Pugettia* spp. (< 20 mm carapace widths), *Fusitriton oregonensis* and *Nucella* spp. (< 0.01·0.25 m^{-2}), and *Cucumaria* spp. (< 0.01·0.25 m^{-2}) were collected but not included in any analysis because they either were rare or below the minimal size threshold for sea otters.

Live prey biomass was significantly lower at used sites than unused sites (Table 4, ANOVA, n = 32, F = 92.3, p = 0.01). Unused sites provided 64% of the total biomass of prey collected in the study area, primarily due to the presence of larger and more abundant *Saxidomus*. Differences can also be attributed to assemblages of non-*Saxidomus* clams including heavier bodied *Macoma* and *Mya* associated with finer grained available sites. *Telmessus* was the largest crab sampled in the study (mean carapace width of 42.6 ± 24.45 mm) and provided greater biomass per unit area in used habitats when present.

Small urchins (mean test diameter of 35.6 ± 15.4 mm) and loosely aggregated mussels provided more biomass per unit area at used sites than at unused sites.

Prey Energy Density - Foraging sites used by sea otters provided significantly less potential prey energy density per unit area than was available at unused sites (Table 5, ANOVA, n = 32, F = 106.4, p = 0.01). Unused sites provided approximately two times more potential energy density per unit area than used sites, primarily due to abundant large-bodied clams. *Saxidomus* were the most energy dense prey species sampled, followed by *Macoma*, *Mya*, and *Leukoma*. *Telmessus* were the most energy dense non-clam prey and provided the highest potential energy density per unit area at used sites. *Mytilus* provided higher potential energy density in used sites; however, differences between used and unused were not significant (ANOVA, n = 32, F = 2.36, p = 0.6). Other mobile invertebrates, including *Cancer*, *Oregonia*, and *Strongylocentrotus* provided consistently low levels of potential energy per unit area across grain sizes.

Discussion

Foraging sea otters consistently used rockier and more topographically complex habitats in this study. Sea otters foraged in larger grain sizes in 94% of used vs. unused site comparisons and used more rugose habitats in 100% of selections. Site selection, however, was not attributable to the highest available prey abundance, biomass, or potential energy density per unit area. Used sites supported significantly fewer, less

calorically rich and, in the case of bivalve species, smaller size distributions of prey than unused sites. Thus, sea otters appear to respond to fine scale variation in sediment composition and sea floor rugosity and forage selectively in heterogeneous benthic environments based on prey accessibility and not on the absolute energy density of potential prey per unit area. Factors other than prey abundance are important in determining sea otter foraging site selection. This study provides evidence for use of epifaunal and infaunal prey resources disproportionate to their availability and potential energy density as has been suggested for sea otters elsewhere in their range (VanBlaricom 1988, Kvitek et al. 1993). In heterogeneous environments, sea otters appear to select resources based on ease of access to prey.

Used sea otter foraging locations consisted of cobble, boulder, and gravel habitats, each more topographically complex than their unused site pair. Preference for more complex habitats has been shown in many organisms including benthic invertebrates (Sebens 1991, Daly and Konar 2008), demersal fishes (Marliave 1977, McCormick 1994, Hamilton and Konar 2007), and marine mammals (Ban and Trites 2007) and can be attributed, in part, to proximity to prey resources (Raffaelli and Hughes 1978, Suryan and Harvey 1998). Unused habitats in this study consisted of smaller grain sizes and less complex habitats including sand, gravel, cobble, and mud. Two biological processes increased surface complexity in unused sites, including the deposition of clam shells through sea otter predation and natural mortality and the maintenance of foraging pits by sea otters and *Pycnopodia helianthoides.* Both shell matter and pits were detected in rugosity measurements in this study and further support the secondary role of sea otters

as disturbers and enhancers of seafloor complexity in sedimentary environments (Kvitek and Oliver 1988, Kvitek et al. 1992). Grain size and rugosity values were significantly correlated at the sampling scale used in this study (see Beck 2000) and are the primary source of substrate complexity in this system, as has been previously described in the study area (Hamilton and Konar 2007, Daly and Konar 2008) and elsewhere (Bourget et al. 1994). The consistent use of larger grain sizes and more rugose habitats by foraging sea otters in this study is likely due to the positive relationship between habitat complexity and local epibenthic species abundance and diversity (Bell et al. 1991).

Sea otter cracked shells were significantly larger, more abundant, and less recently cracked at unused sites than at used sea otter foraging sites in this study. This finding suggests two important observations related to prey use and resource selection in the study area. The first observation, based on greater shell abundance, indicates intense selection of unused sites prior to the study period. Otter cracked shell abundances at unused sites during this study resembled those reported in long-occupied sea otter sites (> 25 years) from a soft sediment system elsewhere in Alaska (Kvitek et al. 1992), suggesting long standing historical use of currently unused sites since occupancy in the study area. This is further supported by longer time estimates since predation in the shell record at unused sites. It is possible that a greater percent of freshly cracked shells at used sites is an indication of increased predation on smaller, less accessible but more structurally confined clams associated with larger grain sizes (Hines and Comtois 1985). Other studies have shown that sea otters, having depleted more easily accessible clams in

adjacent soft sediment habitats, are more likely to remove boulders and excavate rocky sediments for prey (Kvitek and Oliver 1992).

The second observation, based on comparisons of mean shell size in the otter cracked shell record and the live prey assemblage, indicates intense size selective predation by sea otters. Sea otter prey size has been shown to vary inversely with duration of sea otter occupancy (Estes et al. 1978) and given the ≥ 50 yr residency of sea otters in the study area following recovery from the fur trade in the 1800's (Schneider 1976), an increasing sea otter population has likely limited clam size. In this study, the shell record consisted of significantly larger otter cracked shells than live clam shells in both used and unused habitats. Very few living *Saxidomus* excavated in any habitat type in this study were as large as the smallest sea otter cracked shells on the seafloor around them. There are, however, several alternative explanations for this size discrepancy, including (1) larger shells are more likely to persist than smaller and/or thinner shells in the shell record due to increased deposition of calcium carbonate with increasing shell length and inflation (Boulding 1984, Kvitek et al.1993), (2) sea otters can consume small clams with their shells, removing them from the shell record (Garshelis 1983, VanBlaricom 1988), and (3) sampling efforts are limited by suction dredge techniques and may not be effective in overcoming adult clam escape rates (Peterson and Andre 1980). The living assemblage of *Saxidomus* was notably size limited with mean clam sizes near the minimal size threshold for predation by sea otters (Estes et al. 1981, Kvitek and Oliver 1988) further indicating long residency time and size selective predation on this clam species in the study area. Non-*Saxidomus* shells were discarded in comparably

low densities in both used and unused habitats, possibly indicating habitat refuge in association with large grain sizes and/or low density refuges in finer grain sizes.

Foraging sea otters did not use sites with the highest abundances of live prey in this study. Unused sites supported significantly more individuals per unit area than used sites, largely due to high abundances of infaunal clams. Differences observed between used and unused sites were primarily due to *Saxidomus* abundance in finer grain sizes in association with mixed assemblages of *Macoma, Mya,* and *Leukoma*. In contrast, used foraging sites were characterized by comparatively low abundances of infaunal clams and dispersed epifaunal prey. Infaunal clams persisted in larger grain sizes but were notably smaller, shallower in the sediment horizon, and less densely aggregated. It is possible that non-*Saxidomus* species persist in a low-density refuge from predation amidst larger *Saxidomus* clams, as has been shown elsewhere among burrowing bivalves (Lipcius and Hines 1986). In addition to low densities of clams, used sites supported patchy abundances of *Telmessus*, *Mytilus* and individual *Strongylocentrotus* often at or below the minimal size threshold for predation by sea otters (20 mm, Estes and Duggins 1995). Unlike mobile epibenthic prey, clam species were able to persist under predation in both used and unused habitats through shallow burial (10-15 cm) within larger grain sizes or deep burial in soft sediments ($\geq$ 20 cm).

The relative paucity of crabs, mussels, and urchins in the presence of sea otters is supported by studies elsewhere in the sea otter range in the North Pacific (Estes et al. 1978, Fanshawe et al. 2003, Laidre and Jameson 2006). The urchin *Strongylocentrotus droebachiensis* in particular has been recognized as an initially rich but short-term food

source compared to clams as has been shown in soft sediment habitats in southeastern Alaska (Kvitek et al. 1992). Sea otters transplanted to Chicagof Island, Alaska rapidly eliminated sea urchins but remained in the area feeding on infaunal clams (Rosenthal and Barilotti 1973). This pattern is consistent with the hypothesis that sea otters switch to less preferred prey as calorically rich and abundant prey are depleted (Ostfeld 1982). Crab and mussel biomass are likely similarly depleted by sea otters preferentially selecting rich and easily captured prey. *Telmessus cheiragonus*, the largest non-clam prey species encountered in this study, are conspicuous, easily captured during prey sampling, and are likely an important factor in sea otter foraging site selection. *Telmessus* exhibit strong inter-annual variability in their recruitment in the study area, single cohorts were notably abundant in the spring and summer of 2008 and 2010 and were largely absent in 2009, as has been reported in the study area and elsewhere for this and other brachyuran species (Daly and Konar 2010). Pulses in the abundance of *Telmessus* likely supplement low densities of both other epibenthic and infaunal prey in this area. Sea otter use of larger grain size habitats is likely due to the initially plentiful mussel and urchin populations and the periodic recruitment and retention of adult crabs. Site selection seems therefore based on accessibility and not on spatially or temporally persistent prey biomass.

The effort required to capture prey is an important factor in predicting foraging site selection and determining the relative profitability of prey (Pyke 1984, Stephens and Krebs 1986). The most profitable prey or prey patch are not always the most targeted due to high energetic costs associated with access and handling time. For example, the deep burrowing behavior of the clam, *Panope abrupta,* significantly decreases its value as prey

to sea otters despite their uncommonly high energy density and biomass per individual (Kvitek et al. 1993). Sea otters have also been shown to preferentially forage on small shallow buried prey versus much larger, but more deeply buried individuals of the same species (Kvitek et al. 1988). Prey preference ranking (Kvitek and Oliver 1988, Kvitek et al. 1989) among sea otters is determined by factors such as prey size and caloric content and mediated by factors such as prey accessibility and handling time. Sea otter diets include a diverse array of prey species that require distinct search and handling behaviors (Estes et al. 2003, Tinker et al. 2008). The preference for certain prey species and the use of prey-specific foraging skills are generally learned or transmitted along matrilines and can lead to specialization for certain food resources (Estes et al. 2003). Pressure to switch between prey species, either due to increasing sea otter numbers or direct competition with other consumers, may not be adaptive if it entails the development of a new set of foraging skills (Cunningham and Hughes 1984). Sea otter selection of low density epibenthic resources in this study could reflect behavioral specialization and provide the highest possible realized profitability for these otters despite abundant infaunal resources. This hypothesis is supported by the dominance of mussel (41%) and crab (31%) in sea otter scats collected in the study area (Doroff et al. 2009).

During the study period, sea otters used habitats with significantly lower measured prey energy density per unit area compared to unused sites. Used foraging locations were characterized by patchy crab resources and low densities of relatively smaller clams. Where available, *Telmessus* was the most calorically rich of the non-clam prey resources, providing consistent but low levels of energy per unit area in cobble and

boulder habitats. In contrast, the highest energy density individuals in unused sites were largely infaunal. Gravel was the most energetically profitable grain size in the study area due to the co-occurrence of large and abundant *Saxidomus* supplemented by patchy low level abundances of *Cancer* and *Telmessus*. Sand and mud habitats provided the second and third highest prey energy per unit area values, respectively, due to consistent abundances of all clam species. The low use of energy-rich clam resources observed in this study could potentially be attributed to sexually segregated preferences for certain prey species among sea otters. Foraging for clams is energetically expensive and is often only undertaken by male sea otters (VanBlaricom 1988, Kvitek et al. 1993). Given the dominantly female use of the study area, it is possible that clam predation remains sexually segregated and is periodic (e.g., occasional entry by males) or is non-segregated and seasonal (e.g., females resort to clam predation when confined in the study area during winter storms). The tagged sea otters in this study did not select foraging sites with the highest potential energy density per unit area. This strategy has been reported among foraging marten (Thompson and Colgan 1990) and hunting dingoes (Corbett and Newsome 1987). Martens employ a foraging strategy that results in encounters with small prey (mice and voles) that provide energy at minimal cost between captures of large prey (rabbits). Dingoes also employ a foraging strategy that ensures that some food is captured, regardless of size, between less frequent kills of large prey. It is possible that sea otters employ a similar strategy where, during searches for high value prey (e.g. large urchins), low value prey (small and/or dispersed mussel, urchin, and crab species) are encountered, handling time is minimal, and therefore very little time is lost searching for

larger prey. Thus, the abundance of low value prey could compensate for their low value (Stephens and Krebs 1986). Such behavior is particularly efficient during periods when large species are less available or more difficult to capture (Thompson and Colgan 1990). This strategy would serve sea otters well in an environment with depleted calorically rich and easily captured prey, plentiful buried prey, and patchy epifaunal prey and could result in the selection of foraging sites typified by less abundance, biomass, and energy density of available prey.

Summary

In support of the first hypothesis, foraging sea otters consistently selected rockier and more complex habitats over finer grained sediments in a heterogeneous environment. Foraging site selection, however, could not be attributed to higher prey abundance, biomass, or energy per unit area as was predicted in the second hypothesis. The differential use of habitat and prey resources was based on prey accessibility and not on prey abundance or absolute energy density of potential prey. Prey resources in this study area are comparable to sites with long-term sea otter residency (Kvitek et al. 1992, Doroff and DeGange 1994). Epifaunal prey species occur in notably low densities indicated by the absence of large crabs, urchins, and clams comparable in size to the shell record. Foraging locations sampled in this study were dominated by female sea otters. Of the 44 otters instrumented by FWS (Doroff and Badajos 2009), ten females (of 12 instrumented) were most frequently observed foraging in the study area. The dietary requirements of

female otters and females with dependent pups inhabiting the study area are likely met by low abundances of more easily captured or handled epifaunal prey (maternal care hypothesis, VanBlaricom 1988) or are supplemented by forays into more open water habitats not observed by telemetered otters in this study (A.M. Doroff pers. com.). The fidelity to this study area exhibited by female sea otters could be driven by prey-specific foraging strategies (Estes et al. 2003). Although used and unused foraging sites had comparable three-dimensional structure and lacked complex coastal features suggestive of escape terrain (Sih 1980), the use of this area could also provide seasonal protection from winter storms (Schneider 1976, Agler et al. 1995). The estimated annual rate of increase of sea otters in Kachemak Bay between 2002 and 2008 was 26% per year (Bodkin and Udevitz 1999, Gill et al. 2009), which exceeds the maximum productivity rate for this species (23% per year, Estes 1990). It is likely that these sea otters are increasing intrinsically and via immigration from other areas and that predation rates will increase on benthic resources in this area. Sea otter resource use can be selective in heterogeneous environments and the effects of sea otter foraging on benthic community structure may vary with local patterns in epifaunal and infaunal prey availability.

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Table 1. Grain size distribution at used and unused sea otter foraging sites. Sites are designated as used and unused and distribution is expressed in terms of frequency of occurrence (%FO). N refers to the total number of sites in a particular grain size bin. Grain sizes are presented as mean ± SD.

			Used		Unused	
Site	Wentworth Scale Size bin	N	% FO	Mean Grain Size (mm)	% FO	Mean Grain Size (mm)
Mud	< 0.1 mm	1	0	-	100	0.05 ± 0.01
Sand	0.2 - <2 mm	5	0	-	100	1.2 ± 0.4
Gravel	3 - <64 mm	6	14.3	19.3 ± 15.6	85.7	17.1 ± 13.8
Cobble	65 - <256 mm	12	69.2	129.1 ± 89.3	30.8	145.7 ± 67.1
Boulder	257 - <1524 mm	7	100	809.3 ± 384.1	0	-
Bedrock	>1525 mm	1	0	-	100	1831.2 ± 415.4

Table 2. Species composition and abundance of sea otter cracked bivalve shells.The relative time since predation is designated as fresh (attached adductor muscle) or old (decomposing). Time since predation values (%) do not total to 100% in cases where shells were unable to be assigned to fresh or old categories. NP = none present.

			Saxidomus	Other most common sp.		Time since pred. (%)	
Use	Habitat	N	%	Species	%	Fresh	Old
Used	Mud	41	93	*Leukoma*	5	26	53
	Sand	367	85	*Macoma*	9	19	47
	Gravel	193	91	*Macoma*	7	16	33
	Cobble	155	89	*Macoma*	11	12	41
	Boulder	39	87	*Macoma*	10	10	58
	Bedrock	0	NP	NP	NP	NP	NP
Unused	Mud	156	94	*Mya*	4	7	71
	Sand	1379	79	*Leukoma*	11	11	69
	Gravel	548	88	*Macoma*	8	10	68
	Cobble	586	80	*Macoma*	18	14	51
	Boulder	145	97	*Macoma*	2	8	65
	Bedrock	0	NP	NP	NP	NP	NP
Used		828	89		8	17	47
Unused		2957	87		9	10	65

Table 3. Live prey abundance at used and unused sea otter foraging sites. Abundance (ind·0.25 m^{-2}) is presented as mean ± SD. Prey species include *Saxidomus gigantea (Saxidomus)*, *Telmessus cheiragonus (Telmessus)*, *Strongylocentrotus droebachiensis (Strongyloc.)*, and *Mytilus trossulus (Mytilus)*. Significant differences between used and unused locations for both *Saxidomus* and Other clam species (ANOVA, $p \leq 0.05$) are indicated with *. Other clam species include *Macoma balthica*, *Mya truncata* and *Leukoma staminea*. Other crab species include *Cancer oregonensis* and *Oregonia gracilis*.

	Clams		Crabs			
Habitat/Use	*Saxidomus*	Other spp.	*Telmessus*	Other spp.	*Strongyloc.*	*Mytilus*
Used						
Mud	-	-	-	-	-	-
Sand	-	-	-	-	-	-
Gravel	4.6 ± 2.8	1.6 ± 1.0	0.4 ± 0.6	0.0 ± 0.4	0.2 ± 0.2	0.1 ± 0.2
Cobble	2.2 ± 1.2	1.1 ± 0.8	0.9 ± 0.9	0.3 ± 0.7	0.0 ± 0.0	0.3 ± 0.4
Boulder	1.1 ± 0.9	1.3 ± 0.7	0.7 ± 1.0	0.2 ± 0.5	0.2 ± 0.5	0.7 ± 0.2
Bedrock	-	-	-	-	-	-
Unused						
Mud	11.3 ± 7.6	4.2 ± 2.5	0.3 ± 0.5	0.1 ± 0.3	0.2 ± 0.6	0.1 ± 0.1
Sand	14.5 ± 9.1	2.1 ± 1.8	0.8 ± 1.1	0.3 ± 0.1	0.0 ± 0.0	0.3 ± 0.4
Gravel	7.1 ± 3.8	1.6 ± 1.1	0.1 ± 0.4	0.0 ± 0.5	0.2 ± 0.8	0.2 ± 0.1
Cobble	4.0 ± 2.9	2.2 ± 0.3	0.5 ± 0.6	0.4 ± 0.3	0.0 ± 0.0	0.3 ± 0.5
Boulder	-	-	-	-	-	-
Bedrock	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.7	0.0 ± 0.0	0.3 ± 0.2
Used	2.6 ± 1.5	1.3 ± 0.3	0.7 ± 0.4	0.2 ± 0.2	0.2 ± 0.4	0.4 ± 0.4
Unused	9.2 ± 5.7 *	2.5 ± 2.1 *	0.4 ± 0.5	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.3

Table 4. Live prey biomass at used and unused sea otter foraging sites. Biomass (g·0.25 m^{-2}) is presented as mean ± SD. Prey species include *Saxidomus gigantea (Saxidomus)*, *Telmessus cheiragonus (Telmessus)*, *Strongylocentrotus droebachiensis (Strongyloc.)*, and *Mytilus trossulus (Mytilus)*. Significant differences between used and unused locations for both *Saxidomus* and Other clam species (ANOVA, $p \leq 0.05$) are indicated with *. Other clam species include *Macoma balthica*, *Mya truncata* and *Leukoma staminea*. Other crab species include *Cancer oregonensis* and *Oregonia gracilis*.

	Clams		Crabs			
Habitat/Use	*Saxidomus*	Other spp.	*Telmessus*	Other spp.	*Strongyloc.*	*Mytilus*
Used						
Mud	-	-	-	-	-	-
Sand	-	-	-	-	-	-
Gravel	91.4 ± 79.3	14.4 ± 9.1	13.2 ± 19.7	0.0 ± 2.1	1.3 ± 1.4	0.5 ± 1.3
Cobble	31.1 ± 27.3	9.9 ± 7.2	29.7 ± 28.3	1.5 ± 3.5	0.0 ± 0.0	1.6 ± 2.1
Boulder	15.5 ± 9.1	11.7 ± 6.3	23.9 ± 36.3	1.0 ± 2.5	1.4 ± 3.5	3.5 ± 1.4
Bedrock	-	-	-	-	-	-
Unused						
Mud	131.6 ± 81.7	37.8 ± 22.5	9.7 ± 16.5	0.5 ± 1.6	1.4 ± 4.2	0.5 ± 0.5
Sand	243.1 ± 101.5	18.9 ± 16.2	26.4 ± 36.3	1.6 ± 0.4	0.0 ± 0.0	1.6 ± 1.9
Gravel	106.3 ± 63.6	14.4 ± 9.9	3.3 ± 13.2	0.0 ± 2.5	1.6 ± 5.6	1.4 ± 0.6
Cobble	85.4 ± 68.9	19.8 ± 3.7	16.5 ± 19.8	2.7 ± 1.4	0.0 ± 0.0	2.4 ± 1.3
Boulder	-	-	-	-	-	-
Bedrock	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	2.5 ± 3.4	0.0 ± 0.0	1.5 ± 1.2
Used	45.8 ± 37.5	12.9 ± 7.1	22.2 ± 17.8	1.3 ± 2.4	0.9 ± 2.1	2.0 ± 1.6
Unused	113.7 ± 93.4 *	22.7 ±12.8 *	13.9 ± 9.9	1.4 ± 1.9	0.7 ± 3.1	1.5 ± 1.2

Table 5. Live prey energy density at used and unused sea otter foraging sites. Energy density (kcal·m^{-2}) is presented as mean ± SD. Prey species include *Saxidomus gigantea (Saxidomus)*, *Telmessus cheiragonus (Telmessus)*, *Strongylocentrotus droebachiensis (Strongyloc.)*, and *Mytilus trossulus (Mytilus)*. Significant differences between used and unused locations for both *Saxidomus* and Other clam species (ANOVA, $p \leq 0.05$) are indicated with *. Other clam species include *Macoma balthica*, *Mya truncata* and *Leukoma staminea*. Other crab species include *Cancer oregonensis* and *Oregonia gracilis*.

	Clams		Crabs			
Habitat/Use	*Saxidomus*	Other spp.	*Telmessus*	Other spp.	*Strongyloc.*	*Mytilus*
Used						
Mud	-	-	-	-	-	-
Sand	-	-	-	-	-	-
Gravel	611.2 ± 530.3	58.4 ± 36.9	56.7 ± 84.6	0.1 ± 6.5	1.5 ± 1.7	2.9 ± 7.7
Cobble	207.9 ± 182.5	40.1 ± 29.2	127.6 ± 121.6	4.6 ± 10.8	0.0 ± 0.0	9.5 ± 12.5
Boulder	103.6 ± 60.8	47.5 ± 25.5	102.7 ± 156.1	3.2 ± 7.7	1.6 ± 4.1	20.8 ± 8.5
Bedrock	-	-	-	-	-	-
Unused						
Mud	880.1 ± 546.3	153.4 ± 91.3	42.1 ± 70.9	1.5 ± 4.9	1.7 ± 5.0	2.9 ± 3.1
Sand	1625.7 ± 678.8	76.7 ± 65.7	113.4 ± 155.2	4.9 ± 1.2	0.0 ± 0.0	9.6 ± 5.4
Gravel	710.9 ± 425.3	58.4 ± 40.1	14.1 ± 56.7	0.1 ± 7.7	2.1 ± 6.7	8.5 ± 3.7
Cobble	571.1 ± 460.7	80.3 ± 15.0	71.0 ± 85.1	8.3 ± 4.3	0.0 ± 0.0	14.4 ± 7.7
Boulder	-	-	-	-	-	-
Bedrock	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	7.7 ± 10.5	0.0 ± 0.0	8.9 ± 7.1
Used	306.2 ± 250.9	52.3 ± 28.8	95.4 ± 55.0	4.0 ± 7.4	1.1 ± 2.5	11.1 ± 9.6
Unused	760.3 ± 624.6 *	92.1 ± 51.9 *	59.7 ± 43.9	4.3 ± 5.8	0.8 ± 3.7	8.7 ± 7.2

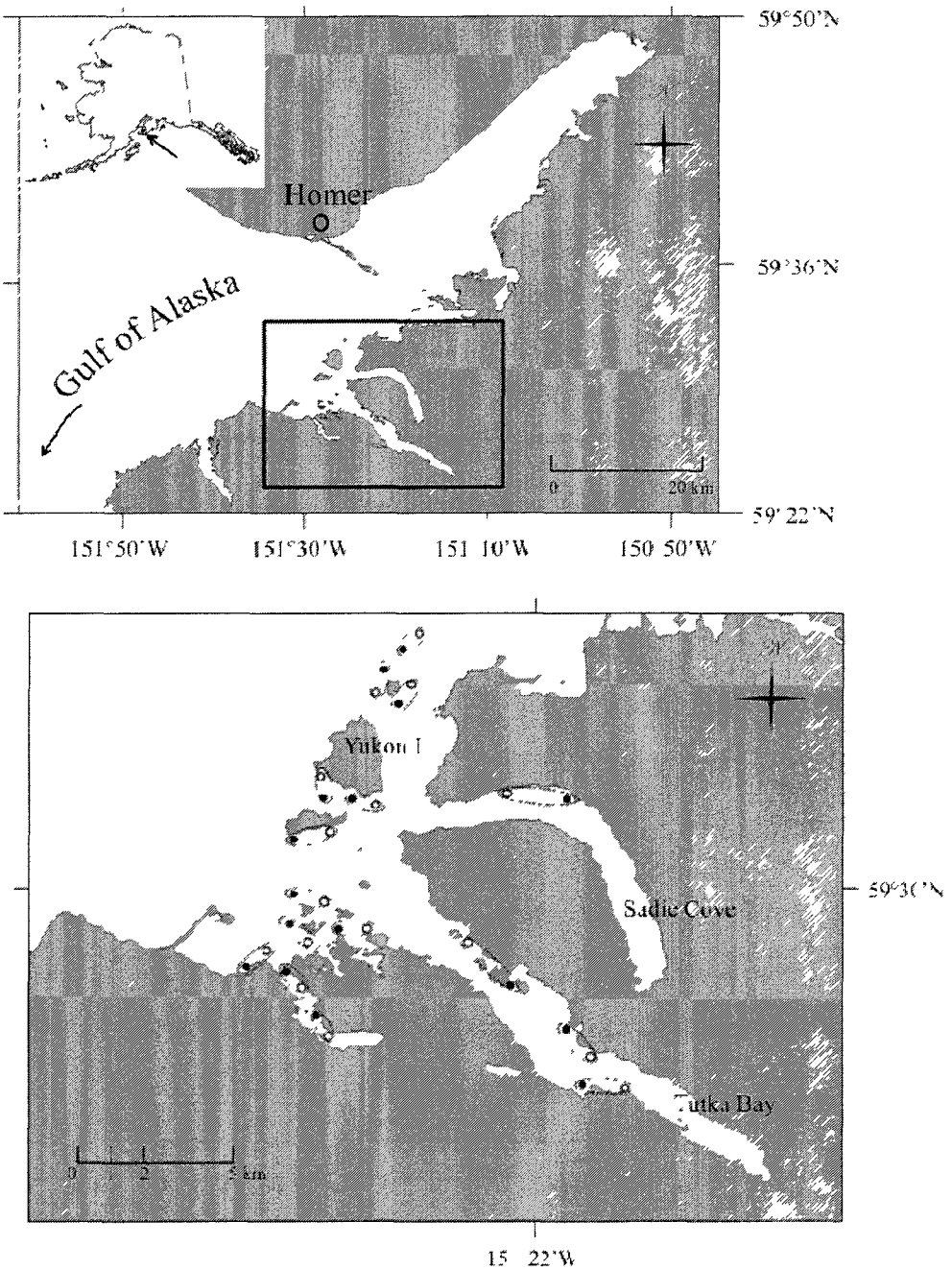

Figure 1. The study area in Kachemak Bay, lower Cook Inlet, Alaska. Used sea otter foraging sites (closed circles) were located by aerial observations of VHF tagged sea otters in a concurrent study (AM Doroff, FWS). Unused sites (open circles) are locations not used by sea otters during the tagging study, Aug 2007 to Feb 2009.

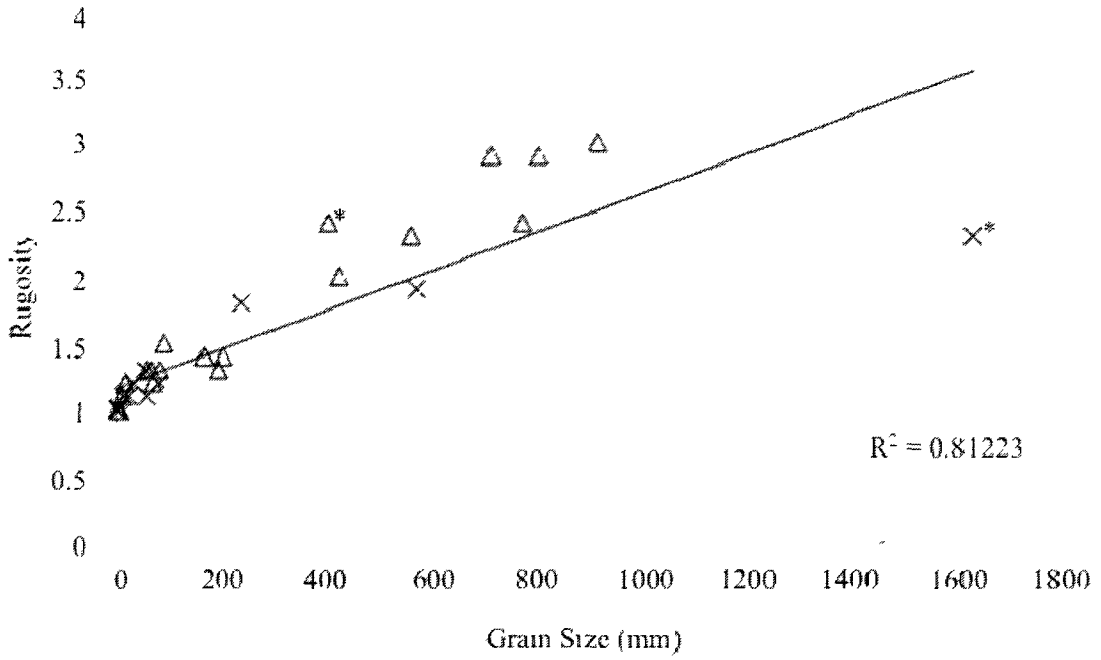

Figure 2. Pearson correlation between grain size and rugosity. Sixteen pairs of used locations "Δ" and unused locations "X" were sampled during the study period. The outlying unused site (*) is a continuous bedrock slope with low surface relief located in an inner fjord, its pair is also indicated. Removal of this site pair from the correlation results in $R^2 = 0.95428$.

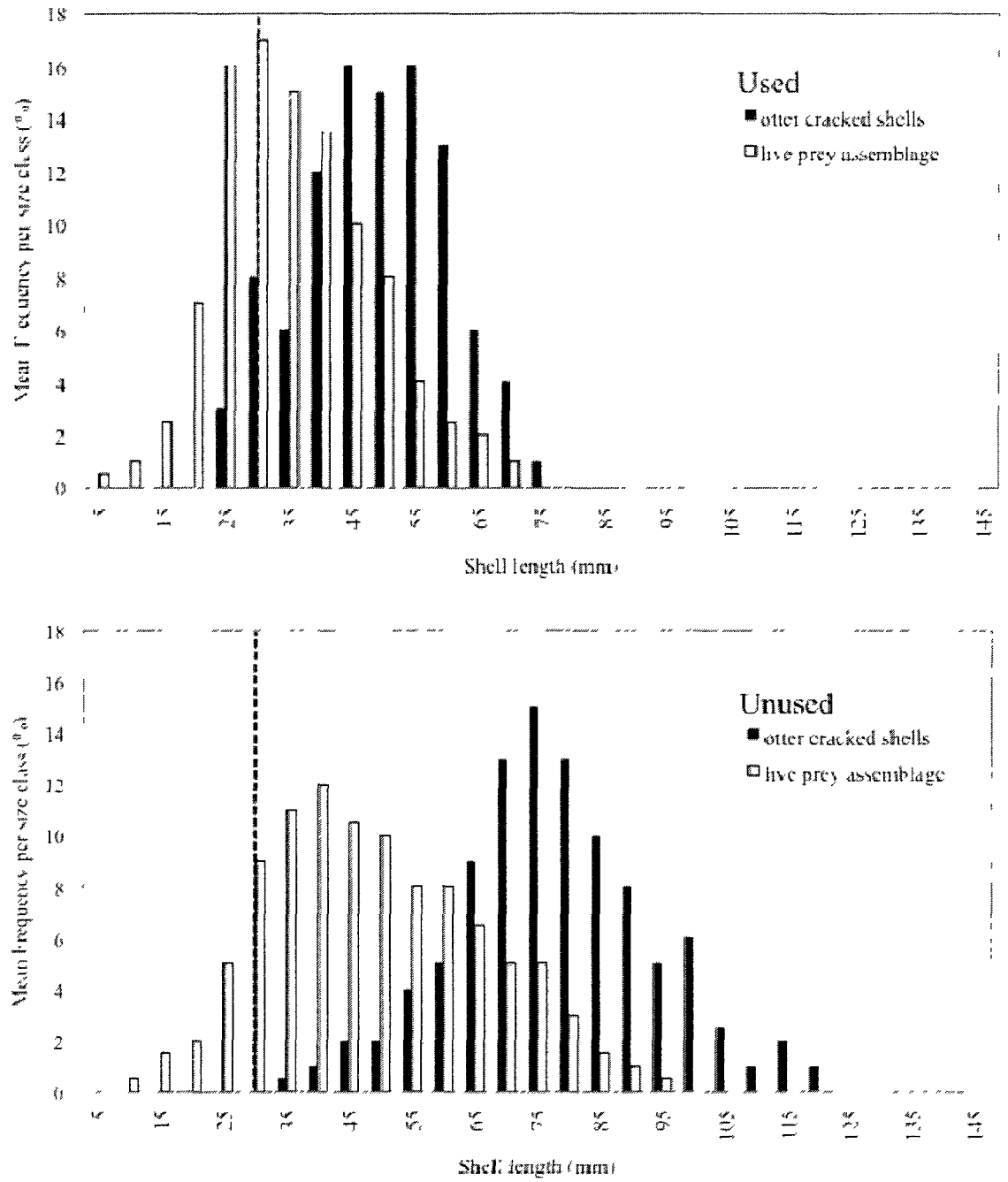

Figure 3. Size distributions of *Saxidomus gigantea* at used and unused sites. Sea otter cracked shells (closed bars) and compared to shells from the live prey assemblage (open bars). Mean frequencies from each size interval were calculated from arcsine-transformed percentages from each site within a given interval. The dotted line indicates the minimum size threshold for predation by sea otters on *S. gigantea* (30 mm).

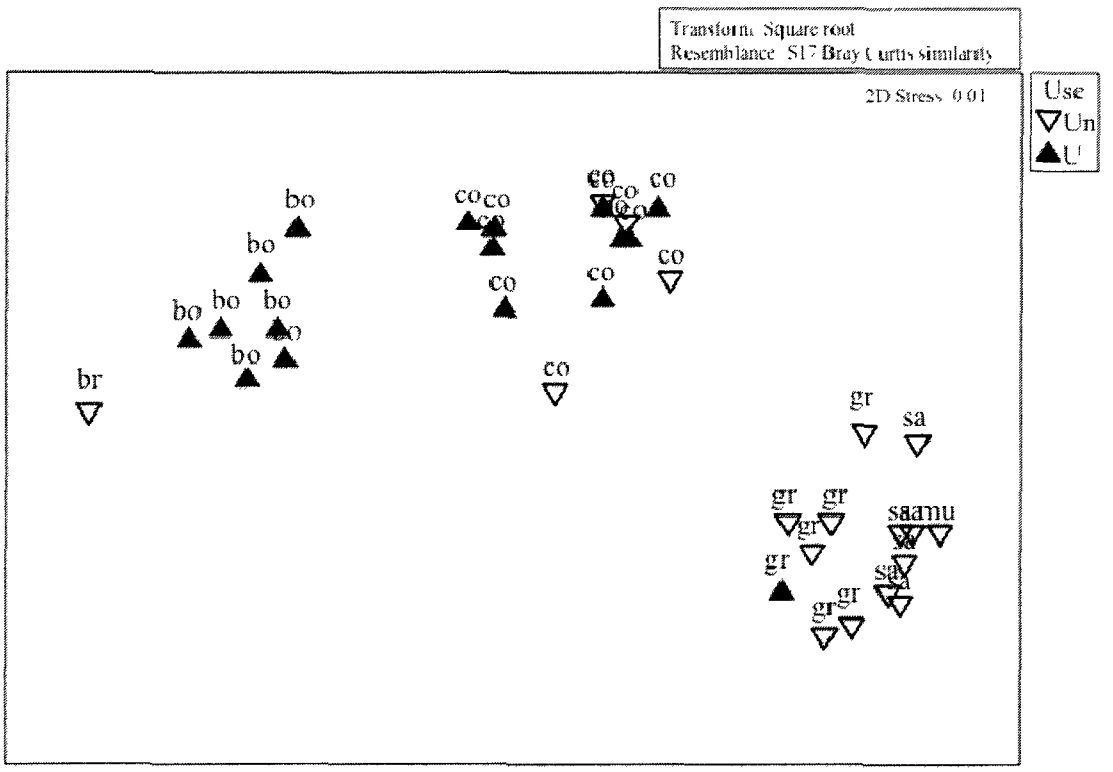

Figure 4. MDS ordination of prey size, abundance, biomass, and energy density. Used (*U*, closed triangle) and unused (*Un*, open triangle) sites are indicated by habitat type; mud (mu), sand (sa), gravel (gr), cobble (co), boulder (bo), and bedrock (br).

CHAPTER 3

Kelp forests vs. urchin barrens: alternate stable states and their effect on sea otter prey quality in the Aleutian Islands[1]

Abstract

Macroalgal and urchin barren communities are alternately stable and persist in the central and western Aleutian Islands due to sea otter presence and absence. In the early 1990's a rapid sea otter population decline released sea urchins from predation and caused a shift to the urchin dominated state. Despite increases in urchin abundance, sea otter numbers continued to decline. Although debated, it has been suggested that the initial sea otter decline and current status are a result of prey quality changes. This study examined sea otter prey abundance, size, biomass, and potential energy density per individual prey species and per unit area in remnant kelp forest and urchin dominated communities in the central and western Aleutians to determine if alternate stable states affect prey quality. Prey quality values were compared to values from elsewhere in the North Pacific with stable or increasing otter populations to determine if nutritional limitation in the Aleutians is occurring. Prey abundance, size, and caloric density were related to sea otter metabolic rate and activity budget to calculate the predicted feeding

[1]Stewart NL, Konar B, Kelp forests vs. urchin barrens: alternate stable states and their effect on sea otter prey quality in the Aleutian Islands, submitted to the Journal of Marine Biology.

effort required to meet daily energy requirements foraging in each community type. Findings suggest that although urchin barrens provide more abundant urchin prey, individual urchins are smaller and provide lower biomass and potential energy density compared to kelp forests. Differences were small however, and overall values were comparable to prey from elsewhere in the sea otters range. Conversely, urchin barrens provide higher biomass and potential energy density per unit area. Shifts to urchin barrens do affect prey species quality but these changes are likely compensated by increased prey densities and are not sufficient to explain the sea otter decline or current status in the central and western Aleutians.

Key words: alternate stable states, prey quality, nutritional limitation, sea otter decline.

Introduction

Natural communities can exist at multiple stable points in time or space (Lewontin 1969). Stable points are characterized by a specific structural and functional species assemblage recognizably different from other assemblages that can occur under the same set of environmental conditions. Such states are non-transitory, persist over ecologically relevant timescales and are therefore considered domains of stable equilibrium (Holling 1973, May 1977). Although multiple stable states can exist simultaneously, communities typically alternate from one stable state to another, a shift often conveyed by a large perturbation applied directly to the state variables (e.g., population densities; Sutherland 1974). Significant changes in the abundance of key species are widely cited as evidence of phase shifts (Beisner et al. 2003, Folke et al. 2004, but see Bertness et al. 2002) and have been documented both experimentally (Paine 1966) and empirically (Knowlton 1992, Mumby et al. 2007) in coastal marine ecosystems. In general, predator removal causes prey community shifts enabling one or few algal or invertebrate competitive dominants to proliferate.

In ecological studies in the Aleutian Islands, the presence and absence of dense sea otter populations can instigate state shifts between two alternately stable nearshore communities, one dominated by kelp and the other by sea urchins (Estes and Palmisano 1974, Dayton 1975, Simenstad et al. 1978). With sea otters present, sea urchins are reduced to sparse populations enabling kelps to flourish. With sea otters absent, dense sea urchin populations overgraze and exclude foliose macroalgae. In the early 1990's a rapid

sea otter population decline caused a shift in alternate stable states in the region, resulting in much of the nearshore rocky ecosystem to be dominated by urchin barrens and largely devoid of macroalgae (Estes et al. 1998, Doroff et al. 2003). Although urchin biomass increased during the decline (Estes et al. 1998), the sea otter population continued to decline and has remained at low densities in the two decades since (Doroff et al. 2003, Estes et al. 2005). Although the cause of the initial decline remains debated (starting with Estes et al. 1998, Springer et al. 2003, DeMaster et al. 2006), it has been suggested that both the decline and the current status of the central and western Aleutian sea otters are a result of prey quality changes (Kuker and Barrett-Lennard 2010). Sea otter diets at the population level are diverse (Estes et al. 2003) and it is argued that nutritional stress arising from changes in prey quality rather than prey quantity has not been sufficiently tested (Kuker and Barrett-Lennard 2010). Nutritional limitation is one explanation for the decline of Steller sea lions (Alverson 1992, Trites and Donnelly 2003) and other marine predators (Österblom et al. 2008) in the North Pacific and Bering Sea based on a shift from energy-rich prey to abundant energy-poor prey (the junk food hypothesis; Alverson 1992, Rosen and Trites 2000). The degree to which shifts between kelp forests and urchin barrens affect prey quality and whether or not such changes could have initiated sea otter population declines, and continue to limit sea otter recovery in the central and western Aleutians, remains to be evaluated.

Kelp forest systems provide critical resources to nearshore marine communities in the central and western Aleutian Islands and throughout the temperate coastal zones (Mann 1973, Cowles et al. 2009). Principal resources include physical structure (habitat)

and food (both directly and indirectly). Kelp forests dampen wave propagation and can mitigate the associated processes of coastal erosion, sedimentation, benthic productivity and recruitment (Duggins et al. 1990). In addition, kelp canopies can influence interspecific algal competition by attenuating sunlight (Dayton 1985) and creating habitat for low-light adapted species (Santelices and Ojeda 1984). The structural complexity of macroalgal systems provides substratum for numerous sessile animals and algae (Duggins 1980, Dunton and Schell 1987) and habitat for mobile organisms specialized to live and feed directly on the kelp or kelp-associated assemblages (Bernstein and Jung 1980, Bologna and Steneck 1993). Although kelps are highly productive, nutrients are primarily made available through macroalgal detritus (Branch and Griffiths 1988, Duggins et al. 1989), while relatively little kelp production (≤10%) is consumed directly by herbivores (Mann 2000). Thus, kelp systems affect the abundance and biomass of associated species and mitigate ecological and oceanographic processes important to nutrient transfer to higher trophic levels.

Broad-scale kelp deforestation can result from disease, herbivory, or physiological stress (Leighton et al. 1966, Lawrence 1975, Duggins 1980). At lower latitudes, periodic kelp forest deforestation results from oceanographic anomalies in temperature, salinity or nutrients that either kill kelps directly or trigger diseases that become lethal to algae (Dayton 1985, Mann 2000). In contrast, at higher latitudes sea urchin herbivory has been the most common agent of kelp deforestation and, despite morphological and chemical defenses in kelps, often leads to the formation of barren grounds (Lawrence 1975, Breen and Mann 1976, Estes et al. 1978, Bernstein et al. 1981). Intensive sea urchin grazing has

both immediate, direct effects on the algal assemblage and numerous complex indirect effects on the greater community (Kitching and Ebling 1961, Estes and Palmisano 1974, Estes et al. 1978). Although constituent species may remain the same, kelp forest and urchin barren systems support notably different assemblages in terms of species abundance, biomass, size distribution, and individual health (Steinberg et al. 1995, Estes et al. 1998). In general, relatively few epibenthic invertebrates succeed in urchin barrens and sea urchins themselves, the competitive dominant, are likely food limited (Konar and Estes 2003, but see Russo 1979, Harrold and Reed 1985) and size limited (Scheibling et al. 1999, Gagnon et al. 2004). Sea urchin's size limitation in urchin barrens has been attributed to both the natural organization of urchin feeding aggregations (e.g., larger urchins lead feeding fronts in kelp beds and smaller urchins occupy adjacent barren zones; Gagnon et al. 2004) and to poor nutritional resources in barrens (Harrold and Reed 1985). The lack of structural habitat complexity associated with urchin barrens can lead to increased predation and further affect prey abundance, biomass and size. Experimental studies with tethered crabs and observational studies of fishes in kelp beds of varying complexity have shown that predation rates are a function of both kelp presence and architectural complexity. In general, larger and more abundant crabs and fishes are associated with more complex algal structure (Hovel and Romuald 2001, Hamilton and Konar 2007). Consequently, habitats lacking kelp harbor smaller prey and are relatively unproductive compared to those with kelp (Simenstad et al. 1978).

Shifts to urchin barren stable states often entail an ecosystem service and function loss (for review see Folke et al. 2004). This is seen in the nearshore where

decreases in the proportion of kelp to barrens has led to coastal consumer decreases (Duggins et al. 1989), reduced interaction strengths between predatory sea stars and their invertebrate prey (Vicknair 1996), and altered fish abundance and diets (Gaines and Roughgarden 1987). In the Aleutian Islands, kelp removal by sea urchins had negative effects on bald eagle, glaucous-winged gull, benthic-feeding sea duck, harbor seal and fish abundances (Estes and Palmisano 1974, Irons et al. 1986, Reisewitz et al. 2006), declines attributed to poor nearshore energy returns and kelp forest habitat loss. Predator declines initiated by phase shifts have been linked to diminished prey resources in many nearshore marine systems (Knowlton 1992, Petraitis and Dudgeon 1999, Menge and Branch 2001). To date, research focusing on alternate stable states has predominantly used predator abundance, diet analyses or behavior to describe cascading effects associated with shifts to "less-desirable" states (Folke et al. 2004). Very few studies have focused directly on individual prey attribute changes associated with phase shifts. Notable exceptions include documented declines in gamete production (Levitan 1991), prey palatability (Barkai and McQuaid 1988) and altered growth rates (Van de Koppel et al. 2001). Although several studies have used sea urchin gonad indices to test for food limitation in urchins (Harrold and Reed 1985, Konar and Estes 2003), no studies to date have described changes in the biomass, size, and potential energy density of prey associated with shifts between kelp forests ("productive systems") and urchin barrens ("less-productive systems"). The co-occurrence of both remnant kelp forests and urchin barrens in the central and western Aleutians provides an opportunity to evaluate prey

quality in each community and to evaluate the hypothesis that prey quality changes initiated the sea otter decline and continue to limit their recovery.

This study quantified sea otter prey quality in remnant kelp forest and urchin barren communities across a longitudinal gradient in the central and western Aleutians to determine if prey quality is affected by phase shifts and if these changes could feasibly limit sea otter recovery. Three hypotheses were developed: (1) remnant kelp forests will provide greater individual prey biomass than urchin barrens, (2) kelp forests will provide greater prey energy density per unit area than urchin barrens, and (3) sea otters foraging in kelp forests require less predicted feeding effort to meet daily energy requirements than sea otters foraging in urchin barrens. To test these hypotheses, and the feasibility of nutritional limitation, sea otter prey abundance, biomass, size, and energy density were evaluated and then related to a foraging sea otter's daily energetic costs and to prey values from elsewhere in the sea otters range where populations are increasing or stable.

Methods

This study was carried out at eight central and western Aleutian Islands in Alaska (Fig. 1). The study spanned a 460 nautical mile longitudinal gradient, from Atka Island (52° 20' 6N, 174° 7' 1W) to Alaid Island (52° 45' 2N, 186° 5' 8E), which was sampled in June of 2009 and July of 2010. Sites (n = 8) were selected based on the presence of a definitive kelp-barren interface (≥30 m long) containing dense understory kelp (≥5 stipes·m^{-2}). Site depths ranged from 10-15 m and were continuous bedrock or large stable

boulder substratum. Cryptic habitats such as deep crevices or loosely piled boulders capable of harboring small sea otter prey species were rare or absent.

To determine if alternate stable state communities provide similar sea otter prey abundance, size, and biomass, 40 randomly placed 0.25 m^2 quadrats were sampled within urchin barrens (n = 20) and adjacent kelp forests (n = 20) at each island. Kelp stipes occurring within quadrats were counted before sampling to ensure minimum kelp density requirements were met. Sea otter prey species, which included sea urchins (*Strongylocentrotus polyacanthus)*, mussels (*Mytilus trossulus*), rock jingles (*Pododesmus macrochisma*), discordant mussels (*Musculus discors*), and hairy tritons (*Fusitriton oregonensis*) were counted and identified to species. Scat analysis and focal observations suggest that these species are the dominant sea otter prey in the region (Estes et al. 1978, Simenstad et al. 1978). Fishes are a component of sea otter diets in the region but are generally less preferred prey (Estes et al. 1978) and, in the case of smooth lumpsuckers, are episodic in their contribution sea otter diet (Watt et al. 2000) and were therefore not included in this analysis. Prey size was determined by measuring the maximum test diameter or shell length of all prey encountered within each quadrat. In addition to counts and size measurements within quadrats, a subsample of sea urchins (n = 10 per community per island) and other prey species (n = 5 per community per island due to lower abundances) were collected from each quadrat (ADFG Permit No. CF-08-016 and CF-09-028). Only the largest individuals of each species occurring within quadrats were collected to simulate size selective foraging behavior exhibited by sea otters (Ostfeld 1982, Estes and Duggins 1995). Biomass per individual prey species was

determined using test- or shell-free wet weight from collected prey and is expressed in terms of g wet mass (WM) per individual. Biomass per unit area (g WM·0.25 m^{-2}) was calculated using species-specific size to biomass conversion factors (Dean et al. 2002, Oftedal et al. 2007) and calibrated using size to biomass values from specimens collected in this study.

To determine if alternate stable state communities provide similar sea otter prey energy density per individual and per unit area, the caloric content of sea otter prey species was determined using bomb calorimetry. In preparation for ash weighing and caloric content analysis, a random subsample of test- and shell-free wet samples from collected prey (n = 3 per species per community per island) were oven-dried at 110°C for 24 h and finely pulverized into powder. Ashing was carried out in a muffle furnace at 500°C for 4 h. Weight loss from ashing was regarded as organic content and used to express the caloric content in terms of ash-free dry weight (AFDW). Homogeneous dry samples were formed into pellets and calorimetric determinations were made with both a Parr model 6200 Isoperibol bomb calorimeter with an 1108 oxygen bomb and 6510 water handling system. Energy from dry matter (cal·g^{-1} DM) was then multiplied by the proportion of dry matter in the wet mass to express potential energy density in terms of wet mass (kcal·g^{-1} WM) per individual prey. Potential prey energy density per unit area (kcal·g^{-1} WM·0.25 m^{-2}) was calculated using species-specific biomass to energy density conversion factors (Dean et al. 2002, Oftedal et al. 2007) and calibrated using values from specimens collected in this study. Although wet mass is influenced by ash and water

dilution, it is a better representation of the actual prey biomass consumed by sea otters (Oftedal et al. 2007).

To determine if sea otters foraging in kelp forests require less predicted feeding effort to meet the daily energy requirements than sea otters foraging in urchin barrens, sea otter prey variables were compared to the activity budget and metabolic rate of a typical 34 kg male sea otter from the central and western Aleutians (Yeates et al. 2007). Prey abundance, size, and energy density were related to sea otter daily energy requirements to calculate predicted feeding effort required to meet daily caloric needs foraging in each community. Predicted feeding effort was calculated in terms of both percent time needed in a 24 hour period to meet daily caloric needs and in terms of the number of individual urchins needed to meet daily caloric needs. Sea otter prey assimilation efficiency was standardized at 82% efficiency (Costa and Kooyman 1984) and feeding rates were standardized at 1.9 urchins·min^{-1} for kelp forests and 3 urchins·min^{-1} for urchin barrens, respectively (USGS, unpubl. data).

To determine if prey quality values in the central and western Aleutians are limiting current sea otter recovery, potential prey energy density values measured in this study were compared to species-specific energy density determinations from locations where sea otter populations are currently increasing (Kachemak Bay Alaska; Stewart and Konar, unpubl. data, Gill et al. 2009, Glacier Bay Alaska; Bodkin et al. 2003, Oftedal et al. 2007, and San Nicholas Island California; Oftedal et al. 2007, Tinker et al. 2008) or stable (Monterey Bay California; Estes et al. 2003, Oftedal et al. 2007). Direct comparisons between sea otter prey species were made at the species level with the

exception of *Strongylocentrotus polyacanthus* (Aleutians) and *S. droebachiensis* (elsewhere in Alaska and California) due to the similarity of these two species (Biermann et al. 2003).

Data Analysis - Differences in prey abundance, biomass, size, and energy density between communities were examined using ANOVA ($p \leq 0.05$) with communities as treatments (i.e., remnant kelp forests and urchin barrens) and means from quadrats within communities within sites as replicates. When significant effects were found in ANOVA, post-hoc comparisons were made using the Tukey's Honestly Significant Difference (HSD) test. Multivariate analysis was used to illustrate differences in urchin barren and kelp prey communities attributable to prey availability, quality, and size (PRIMER-E v.6, Clarke and Warwick 2001, Clarke and Gorley 2006). Prior to analyses, data were square root transformed to reduce the dominant contributions of abundant species and a similarity matrix of all samples was produced using a Bray–Curtis index. The similarity between urchin barren and kelp communities was assessed in terms of prey variables using multidimensional scaling ordination. Similarity percentages analysis (SIMPER) was used to determine which taxa contributed most to the observed dissimilarity between urchin barren and kelp communities represented by the Euclidean distances among sites.

Results

Kelp forest and urchin barren communities were clearly delineated by differences in kelp and macroinvertebrate abundance (Table 1). Urchin barrens provided significantly more abundant prey than remnant kelp forests (ANOVA, $n = 8$, $F = 132.1$, $p < 0.001$). Tukey post-hoc comparisons indicated that *Strongylocentrotus polyacanthus* was significantly different between kelp forests and urchin barrens. Dense *S. polyacanthus* populations comprised the bulk of available prey (45.5 to 87.9%) in both communities but were seven times more abundant in barrens (28.6 ± 5.8 ind·0.25 m^{-2}) than in remnant kelp forests (3.8 ± 1.9 ind·0.25 m^{-2}). When present, *Musculus discors* was more abundant in kelp forests (0.8 ± 1.1 ind·0.25 m^{-2}) than urchin barrens (none present); however, this species only occurred at three of the eight islands. The rock jingle, *Pododesmus macrochisma*, was consistently abundant at low densities in both communities. The remaining prey species, *Mytilus trossulus* and *Fusitriton oregonensis*, showed patchy distributions or were equally present in both kelp forests and urchin barrens.

Kelp forests supported significantly larger urchins (54.1 ± 21.4 mm) than barren habitats (47.1 ± 17.3 m; ANOVA, $n = 8$, $F = 5.34$, $p = 0.02$; Fig. 2). Additionally, kelp forests provided significantly higher biomass per individual urchin than barrens (ANOVA, $n = 8$, $F = 39.1$, $p = 0.016$; Fig. 3). Urchin barrens, however, provided significantly higher biomass per unit area compared to remnant kelp forests (ANOVA, $n = 8$, $F = 97.9$, $p < 0.001$). Individual urchins in kelp forests provided significantly higher potential energy density (0.21 ± 0.02 kcal·g^{-1} per urchin) compared to urchin barrens

(0.14 ± 0.08 kcal·g^{-1} per urchin, ANOVA, $n = 8$, $F = 26.6$, $p = 0.03$; Fig. 4). In contrast, urchin barrens provided significantly greater potential energy per unit area than kelp forests (ANOVA, $n = 8$, $F = 107.2$, $p < 0.001$). Potential energy density values of individual prey species (kcal·g^{-1} WM·ind.$^{-1}$) from both communities in this study were comparable to values from other studies conducted elsewhere in the sea otters range (Table 2).

A typical sea otter in the central and western Aleutians could easily meet daily energy requirements foraging in either kelp forest or urchin barren communities. A 34 kg male sea otter has a daily energy requirement of approximately 4600 kcal·day^{-1} (Yeates et al. 2007). Due to differences in the abundance, size, and energy density of urchins from remnant kelp forests and urchin barrens, a typical Aleutians sea otter would need to consume 484 urchins in a kelp forest (18% time, feeding rate of 1.9 urchins·min^{-1}) versus 1085 urchins (25% time, feeding rate of 3 urchins·min^{-1}) in an urchin barren to meet daily caloric needs (Oftedal et al. 2007, Yeates et al. 2007). The differences in percent foraging time required to meet daily caloric needs in either community are well below that seen in populations where food resources are limiting, such as central California where male sea otters spent 25-40% time feeding (Yeates et al. 2007, Tinker et al. 2008). In addition, given comparable feeding rates foraging in either community, the number of urchins required to meet daily caloric needs are well within the actual number observed in empirical studies of foraging sea otters (e.g., Watt et al. 2000).

Sea otter prey abundance, size, biomass, and energy density contribute to the separation in urchin barren and kelp forest communities in multidimensional scaling

analyses (MDS; Fig. 5). The separation between communities was driven by significantly higher total prey biomass and potential energy per unit area associated with dense sea urchin populations in urchin barrens (Fig. 6 for biomass, SIMPER, 87%). Individual urchin energy density did not contribute significantly to the separation in sites (SIMPER, 9%).

Discussion

In its current stable state of mostly urchin barrens, the nearshore community in the central and western Aleutian Islands is dominated by abundant but low quality prey. Expansive urchin barrens support dense sea urchin populations that are generally smaller and provide less biomass and energy density per individual than kelp forest urchins. Interspersed in the system is a patchwork mosaic of remnant kelp forests that support relatively few but large, calorically rich individuals. Though statistically significant, the difference in individual sea urchin potential energy density in kelp forests and urchin barrens is likely ecologically inconsequential to foraging sea otters. Potential urchin energy density values measured in this study indicate that an average kelp forest urchin is equal to approximately one and half barren urchins in terms of edible wet biomass and energy content. Given sea urchin feeding rates and assimilation efficiency (Yeates et al. 2007), sea otter daily energy requirements are easily met foraging in either community. Although individual prey quality changes likely occurred during the shift from kelp forests to urchin barrens during the 1990's sea otter decline, these changes are not likely

to have caused the sea otter decline nor are they limiting current sea otter recovery. Both kelp forest and urchin barren urchins sampled in this study are comparable to potential energy density values of individual urchins elsewhere in the sea otter range. In addition, all other sea otter prey evaluated in this study, with the exception of *Musculus discors*, did not vary in abundance, size, biomass, or energy density between kelp and barren communities. Consequently, though changes in prey quality associated with phase shifts represent an ecosystem service loss to predators, this loss is likely compensated by increases in prey abundance and total available biomass.

Sea urchins competitively dominate nearshore communities in the central and western Aleutian Islands. Their dominance in the absence of top-down control is typical of urchin barren phase states elsewhere (Knowlton 1992, Andrew and Underwood 1993) and is comparable to other competitive dominants in marine systems where predators have been experimentally removed, including barnacles (Dayton 1971) and mussels (Paine 1974). Urchin densities in urchin barrens sampled in this study were approximately seven times greater than in remnant kelp forests, a pattern common throughout the Aleutian Islands during phase shifts to urchin barrens (Simenstad et al. 1978, Estes et al. 1998). Kelp forest associated urchins were often found among kelp blades and less commonly observed on the substrate, were larger, and provided significantly more biomass per urchin than urchins in barrens. Urchins associated with barrens, in addition to being smaller, were notably diminished in wet tissue mass and generally contained very little to no reproductive tissue compared to kelp forest urchins. Mass differences between individual urchins were attributed both to size differences and

to differences in the ratio of reproductive to non-reproductive tissue, a variable known to decrease with increasing urchin density (Levitan 1991) and increase with increasing macroalgal food sources (Konar and Estes 2003). Urchin reproductive tissue is significantly more energy dense than other tissues (Andrew 1986) and in this study translated into significantly higher energy density per individual urchin. Consequently, although urchins in kelp forests are significantly less abundant than in urchin barrens, they provided more biomass and potential energy density per individual. Greater sea urchin densities in urchin barrens provide greater total available prey biomass and total potential energy density due to the total mass of tissue available not the mass or quality of tissue per individual. Thus, the relationship between prey availability and quality in these two phase states is more complex than suggested by species abundances alone.

The absence of kelp did not have an effect on the distribution or density of four of the six sea otter prey species sampled during this study. Two prey species, including urchins themselves, varied in abundance with kelp presence and absence. In contrast to the inverse relationship urchins exhibited with kelp, *Musculus discors* was more abundant in kelp due to its preferred association with kelp blades (Waage-Nielson et al. 2003). *Musculus discors* had a non-uniform distribution and occurred in a dense but patchy distribution as seen in recruitment studies elsewhere in the North Pacific (Begin et al. 2004). The remaining sea otter prey species sampled in this study did not show any variation in abundance, biomass, energy density, or size as a function of community type. *Pododesmus macrochisma* provided relatively high biomass and energy density per unit area but did not vary significantly in abundance between communities. This species is

conspicuous, often occurring in dense aggregations on the edges of boulders and on ledges, and is easily removed from the substrate. Both *M. discors* and *P. macrochisma* are utilized by sea otters in the central and western Aleutians (Estes and Tinker unpubl. data) and likely supplement sea urchin energy density when preferred food items such as large sea urchins are scarce (Estes et al. 1981). *Mytilus trossulus* and *Fusitriton oregonensis* exhibited patchy distributions and did not vary significantly between communities. With the exception of the patchy distribution of the kelp-associated *M. discors*, the availability and quality of non-urchin sea otter prey sampled in this study did not vary significantly with kelp presence or absence. The co-variations between *M. discors* abundance and kelp abundance, and *S. polyacanthus* and kelp abundance, suggest that the degree to which phase shifts affect prey quality depends on the interaction strength between a particular prey species, kelp, and kelp subsidies. As a result, sea urchins, a preferred prey of sea otters and directly linked with kelp forest-urchin barren dynamics, are a strong indicator of phase shifts in the Aleutians (Estes et al. 2010). These findings support Estes et al. (1998) use of sea urchin biomass increases as evidence against nutritional limitation as the cause for the sea otter decline. It also addresses the concerns by Kuker and Barrett-Lennard (2010) that additional abundance data for non-urchin sea otter prey species may refute Estes et al. (1998).

Given sea urchin importance to sea otter diets in the central and western Aleutians (Kenyon 1969, Estes and Palmisano 1974, Simenstad et al. 1978), the potential impacts of changes in sea urchin abundance, biomass, size, and energy density between phase states detected in this study deserve closer evaluation. Potential calorie availability in the

central and western Aleutians varies by the prey unit exploited (e.g., individual urchin vs. aggregations of urchins) and by the type of community being targeted. Currently the spatially dominant community in the region, urchin barrens, supplies more nutrition per unit area but less nutrition per individual than kelp forests. Depending on a predator's foraging strategy, foraging for sea urchins in remnant kelp forest patches vs. expansive urchin barrens could provide significantly different potential energy returns (Stephens and Krebs 1986). A predator that preferentially consumes larger and more calorically rich individual prey at the cost of increased search time in kelp understory would benefit from the selective use of kelp forest patches. Cormorants exhibit this foraging strategy in their selection of dense kelp-forested areas as opposed to recently kelp-harvested areas in Norway, despite significant increases in foraging times associated with locating fish in kelp (Lorentsen et al. 2010). This strategy is only feasible until the point at which the nutritional advantages of targeting prey in complex environments is outweighed by the cost of increased search time (Stephens and Krebs 1986). In contrast, a predator that exhibits general foraging behavior would likely exploit urchin barrens habitually and opportunistically forage in kelp forests. This strategy is exhibited by fish-eating killer whales that generally hunt in open water but occasionally specialize their foraging behavior and work cooperatively to take salmonid prey seeking refuge in dense kelp beds (Ford and Ellis 2006). Sea otters are size-selective foragers that generally select the largest and most calorically rich prey first before switching to smaller or less preferred prey species (Ostfeld 1982, Garshelis 1983). Theoretically, a community dominated by small, low quality prey could alter predator movement (Cruz-Rivera and Hay 2000), lead

to abandonment for areas with greater potential energy density (Charnov 1976, Abrams 1984), or result in starvation and population decline; however, given the subtle differences in individual and areal potential energy density, these scenarios are unlikely with sea otters. Sea otters have large energy requirements due to an elevated metabolic rate (Kenyon 1969, Iverson 1972) and as a result ingest 20 to 25% of their body mass in prey per day (Kenyon 1969, Costa and Kooyman 1984) and spend 23 to 50% of the day foraging (Estes et al. 1986, Ralls and Siniff 1990, Tinker 2004). Given the distances sea otters travel during foraging (Garshelis and Garshelis 1984, Estes 1990), sea otter daily caloric needs are easily met foraging in either remnant kelp forest or urchin barren communities. Numerous examples of expanding sea otter populations have reported otters continuing to forage in areas of depleted prey rather than moving to adjacent sites with larger individual prey and higher overall prey abundances (Kvitek et al. 1993, Laidre and Jameson 2006). Furthermore, though depleted individual sea urchin quality values detected in urchin barrens in this study were lower than urchin values from locations where sea otter populations are currently increasing or stable, a difference of such small magnitude (ca. 0.07 $kcal \cdot g^{-1}$) is not likely to affect sea otter resource selection. Consequently, despite the differences in individual prey abundance, biomass, size, and energy density between kelp forests and urchin barrens in the central and western Aleutians today, nutritional limitation is not likely to affect potential sea otter recovery to the region.

In conclusion, the phase shift between kelp forest and urchin barrens not only have an effect on kelp and urchin abundance and biomass but have also further effects on

both individual and total potential energy density provided by urchins. In support of the first hypothesis, remnant kelp forests provide greater individual prey biomass than urchin barrens. Kelp forests do not, however, provide greater energy density per unit area than urchin barrens as was predicted in the second hypothesis. Prey quality differences were, however, not significant enough to explain the rate of sea otter population declines reported during the 1990's (ca. 25% per year; Estes et al. 1998) nor are they sufficient to explain the persistent limitation of sea otter recovery in the two decades since the decline. Given what is known about sea otter foraging behavior, gross daily metabolic needs, and prey availability, it is not feasible that sea otters were or are currently nutritionally limited in the central and western Aleutians. Although the capacity of sea otters to exploit sea urchin hyper-abundance and re-colonize their historical range is indisputable from both practical (Doroff and DeGange 1994, Laidre and Jameson 2006) and conceptual standpoints (Paine 1977), the ecosystem wide effects of alternating between energy-poor and energy-rich equilibrium points likely has effects on resource selection and ultimately the carrying capacity of other consumers in the central and western Aleutians. This study indicates that the overall potential energy density provided by kelp forests is diminished when urchin barrens are temporally and spatially dominant, as has been speculated for urchin barrens elsewhere (Harrold and Reed 1985). Phase shifts in kelp forest-urchin barren systems have effects on the potential prey energy density available to higher trophic levels and, in addition to statistical differences in the abundance of key species, could provide a further means to differentiate between equilibrium states.

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Table 1. Kelp density and prey abundance in kelp and barren communities. N is the mean of prey species counted within 0.25 m^2 quadrats in each community (n = 8 islands with 20 quadrats per community per island). Prey species include *Strongylocentrotus polyacanthus (Strongylo.)*, *Pododesmus macrochisma (Pododes.)*, *Musculus discors (Muscul.)*, *Mytilus trossulus (Mytilus)*, and *Fusitriton oregonensis (Fusitrit.)*. Significant differences from Tukey post-hoc comparisons $p \leq 0.05$ level are indicated by (*). NP = Not present.

	Kelp density		Abundance (ind. 0.25 m^2)				
	(ind.·0.25 m^2)	N	*Strongylo.*	*Pododes.*	*Mytilus*	*Muscul*	*Fusitrit.*
Kelp	5.89 ± 1.14	1.6 ± 1.1	3.8 ± 1.9 *	2.3 ± 1.2	0.9 ± 0.7	0.8 ± 1.1	0.2 ± 0.1
Barren	NP	6.5 ± 2.3	28.6 ± 5.8	2.5 ± 1.5	1.1 ± 0.6	NP	0.3 ± 0.1

Table 2. Prey energy values kelp and barren communities in AK and elsewhere. Values indicate the potential energy density per individual species (kcal·g^{-1} wet mass) ± 1 S.D. Prey species include *Strongylocentrotus polyacanthus*, *Mytilus trossulus*, and *Fusitriton oregonensis*. *S. polyacanthus* is most common in the Aleutians but is compared to *S. droebachiensis* from other regions in this table given their similarity in mitochondrial DNA analysis (Biermann et al. 2003). Current population trends were referenced in Estes et al. 2005 (C. and W. Aleut., AK: central and western Aleutians, AK); Gill et al. 2009 (KBay, AK: Kachemak Bay, AK); Bodkin et al. 2003 (GBNP, AK; Glacier Bay, AK); Estes et al. 2003 (MBNMS, CA: Monterey Bay, CA); and Tinker et al. 2008 (SNI, CA: San Nicholas Is., CA). Sources of regional prey values are (A) this study; (B) Stewart and Konar, unpubl. data; (C) Oftedal et al. 2007. Sea otter population status from each location are either (D) declining; (I) increasing; or (S) stable. NP = Not present.

		Sea otter	Prey Species		
Location	Source	pop. status	*Strongyloc*	*Mytilus*	*Fusitrit*
C., W. Aleut., AK					
kelp forest	A	D	0.21 ± 0.02	0.41 ± 0.06	1.36 ± 0.06
urchin barren	A	D	0.14 ± 0.08	0.47 ± 0.04	1.41 ± 0.03
KBay, AK	B	I	0.26 ± 0.06	0.36 ± 0.02	1.09 ± 0.08
GBNP, AK	C	I	0.24 ± 0.04	0.33 ± 0.06	1.11 ± 0.23
MBNMS, CA	C	S	0.39 ± 0.04	0.55 ± 0.04	NP
SNI, CA	C	S	0.66 ± 0.30	0.29 ± 0.16	NP

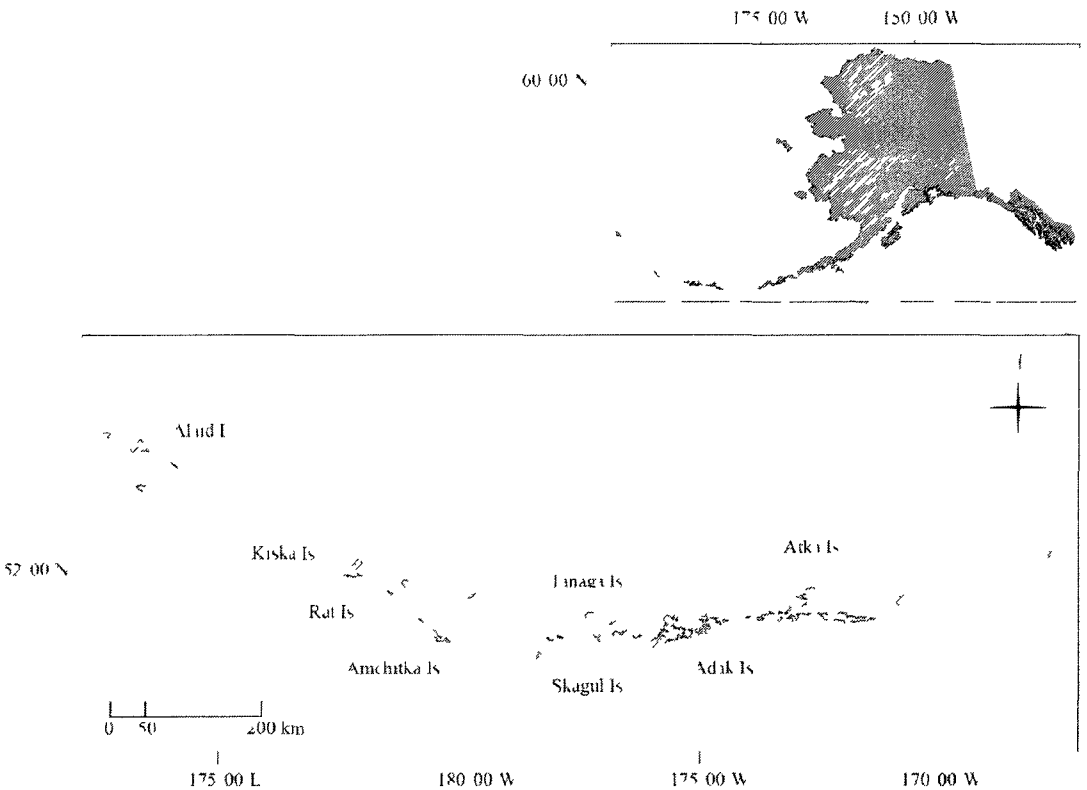

Figure 1. The study area in the central and western Aleutian Islands, Alaska. The eight islands sampled in this study are indicated

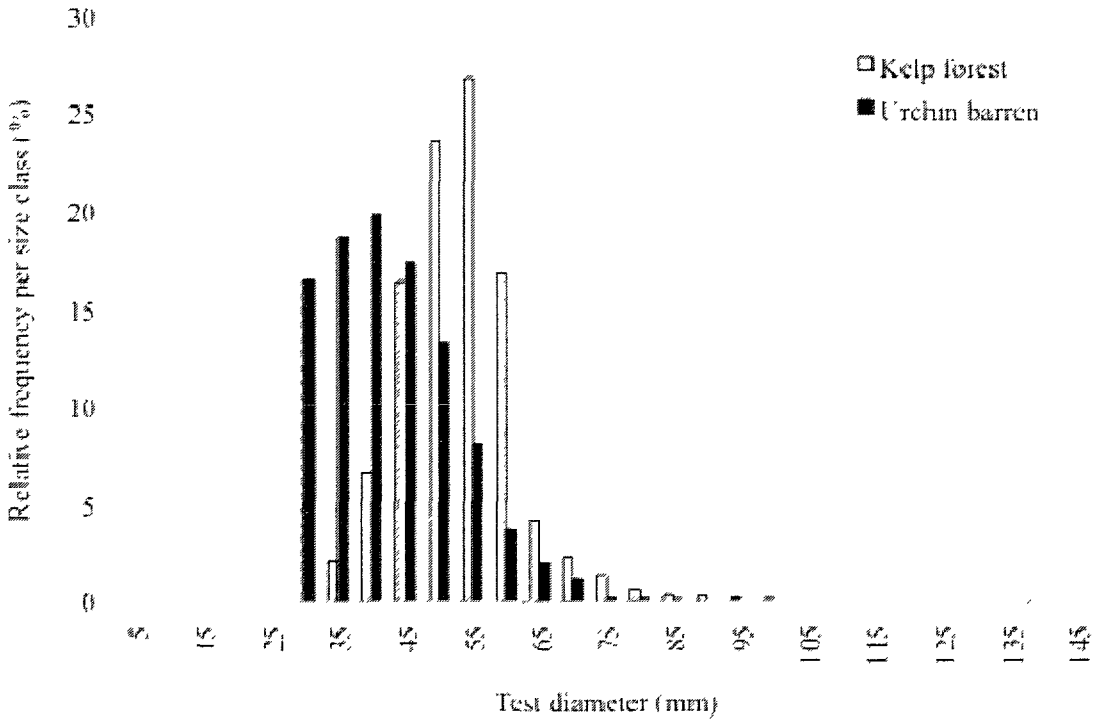

Fig 2. Relative frequency distributions of sea urchins in kelp and barren sites. Relative frequency percentages are determined using counts from sea urchins in kelp forests (n = 308) and urchin barrens (n= 4569). The dotted line indicates the minimum size threshold for sea otter predation on urchins (30 mm).

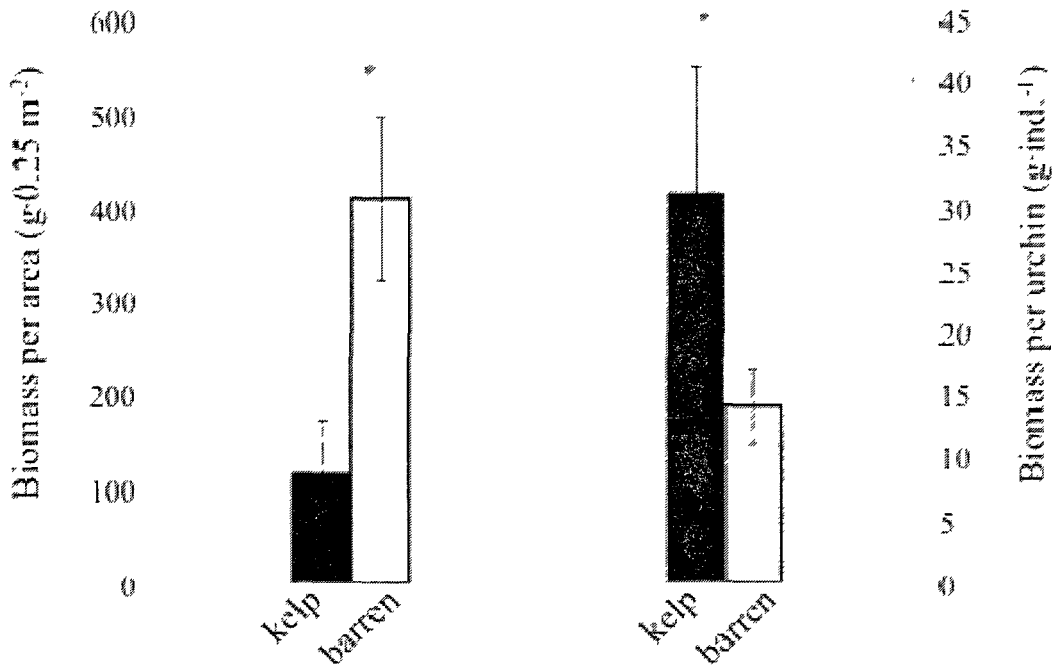

Figure 3. Sea urchin biomass per unit area and individual in kelp and barren sites. Significant differences at $p \leq 0.05$ level are indicated by (*).

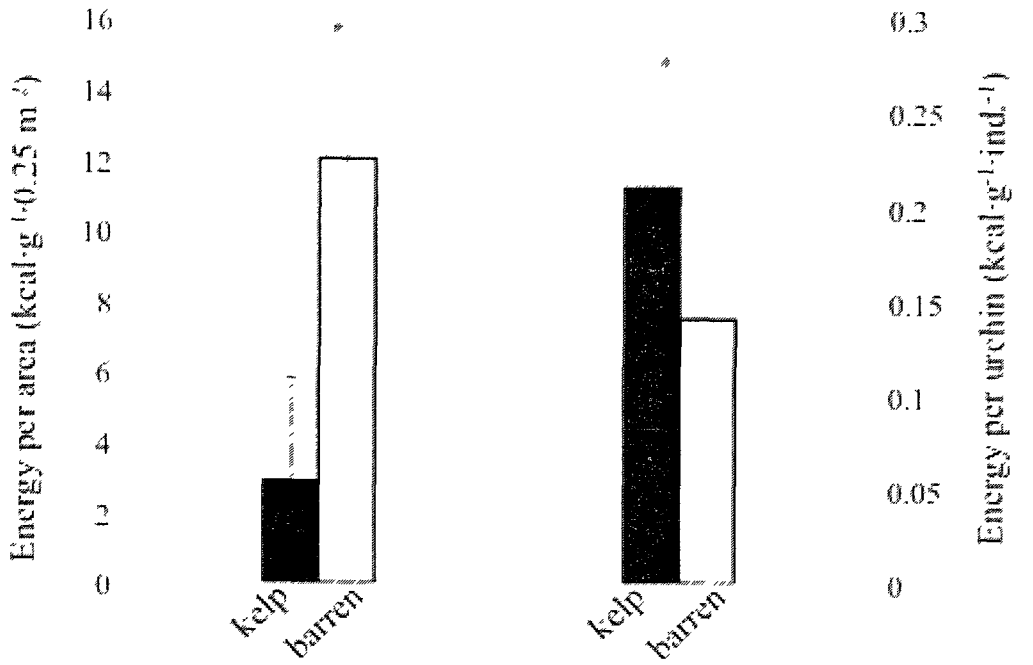

Figure 4. Sea urchin energy per unit area and individual in kelp and barren sites. Significant differences at $p \leq 0.05$ level are indicated by (*).

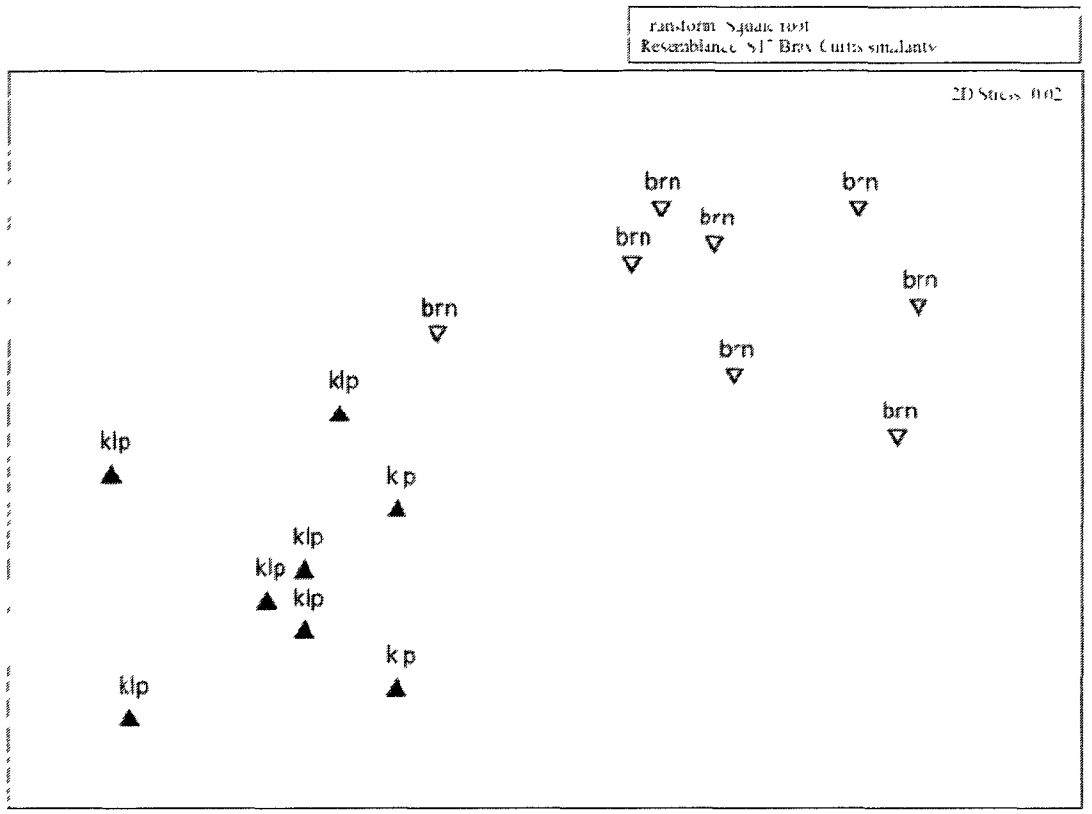

Figure 5. MDS ordination of prey size, abundance, biomass, and energy density. Kelp forests (klp) and urchin barrens (brn) are indicated.

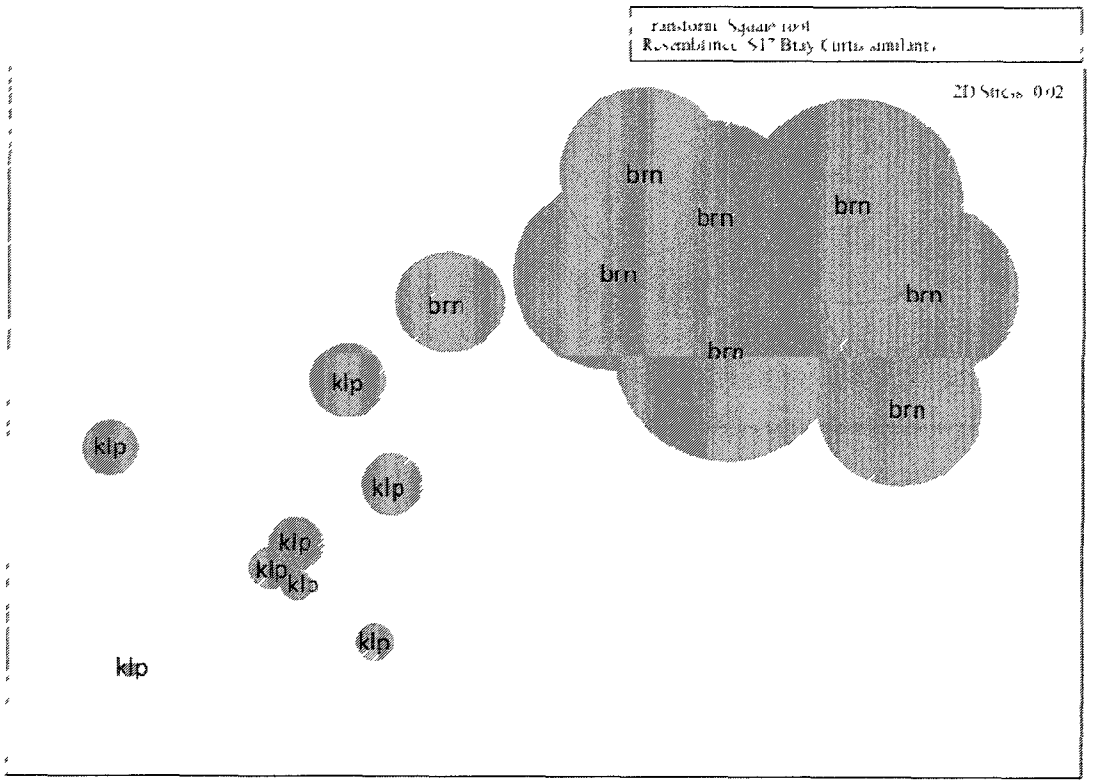

Figure 6. MDS bubble plot of prey biomass kelp and barren sites. Bubble size scales with g·0.25 m^{-2} from remnant kelp forest (klp) and urchin barren (brn) sites.

CHAPTER 4

Testing the nutritional limitation and predator avoidance hypotheses for restricted sea otter habitat use in the Aleutian Islands, Alaska[1]

Abstract

Sea otters inhabiting the Aleutian Islands have stabilized at low abundance levels following a population decline and currently exhibit restricted habitat selection patterns. Causes for sea otter restricted habitat use have manifested in a debate involving two different processes, bottom-up and top-down forcing. Bottom-up hypotheses argue that changes in the availability or nutritional quality of prey resources have led to the selective use of habitats that support the highest quality prey. In contrast, top-down hypotheses argue that increases in predation pressure from killer whales have led to the selective use of habitats that provide the most effective refuge from killer whale predation. A third hypothesis suggests that current restricted habitat use is based on a need for protection from storms, a bottom-up process that can lead to the selective use of habitats that provide the most effective refuge from prevailing weather. This study tested all three hypotheses for restricted habitat use by comparing: (1) prey availability and quality, (2) structural habitat complexity, and (3) exposure to prevailing storms between currently

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used versus historically used sea otter foraging locations. Findings suggest that current use is based on physical habitat complexity and not on prey availability, prey quality, or protection from storms, providing further evidence for predation as a cause for restricted sea otter habitat use in the Aleutian Islands.

Key words: restricted habitat use, prey quality, habitat complexity, predator avoidance.

Introduction

Many factors contribute to the selective use of habitats by animals, including habitat suitability, prey quality, and predation risk (Sih 1987, Lima 1998, Andruskiw et al. 2008). Of particular interest are situations where habitats with high food availability also have high predation risk. Foraging under the risk of predation often results in a fundamental trade-off between food and safety or can lead to the selection of more highly restricted habitats (e.g., shifting activity toward safer but less rewarding food patches; Sih 1980, Brown 1999). In some situations, animals in low abundance may be distributed across habitats proportional to prey availability, as exhibited by guppies (Abrahams and Dill 1989) and armored catfish (Oksanen et al. 1995). In the absence of predators, guppies used restricted habitats based on prey distribution. However, if predation risk varied among habitats, animals did not necessarily select habitats based solely on potential energetic return (Abrahams and Dill 1989). Instead, individuals accepted lower energetic returns to forage in relatively safer habitats. Both theoretical studies on trait-mediated interactions (Bolker et al. 2003) and the evolutionarily stable strategy concept (McNamara and Houston 1992) and empirical studies involving creek chubs (Gilliam and Fraser 1987) and coho salmon (Grand and Dill 1997) have shown that predation pressure results in animals undermatching the relative food availability in dangerous habitats. Preferred salmon habitats are shallow areas with swift currents; however, when avian predators such as kingfishers are present, salmon restrict their habitat use to areas with high stream structure (e.g., rocks and vegetation) or overhead cover (e.g., undercut banks

or fallen logs) despite reduction in foraging gains. Determining the cause of restricted habitat use in populations under potential prey availability-predator avoidance trade-offs entails the investigation of prey distribution, prey quality, and predation risk (Sih 1980, Lima 1998, Heithaus and Dill 2006).

Sea otters currently inhabiting the Aleutian Islands are selecting restricted habitats (Estes and Tinker unpubl. data), a characteristic of populations that have stabilized at low abundances following a decline (Norris 2004). Sea otter populations in the Aleutians declined precipitously during the early 1990's (Estes et al. 1998, National Research Council 1996, 2003) and have not recovered to pre-decline numbers in the two decades since (Doroff et al. 2003, Estes et al. 2005). During the decline, sea otters shifted from the broad use of available nearshore habitats to the selective use of very few nearshore habitats (Estes and Tinker unpubl. data). The causes for this shift, and the sea otter decline in general, remain actively contested (beginning with Estes et al. 1998) and have manifested in a debate involving two fundamentally different processes, bottom-up and top-down forcing (National Research Council 2003). In general, bottom-up forcing hypotheses posit that sea otters are nutritionally limited and that restricted habitat use is due to changes in the availability or quality of prey. In contrast, top-down hypotheses posit that restricted habitat use is predator mediated due to increases in killer whale predation pressure. Changes in prey quality can result in altered consumer movement (Cruz-Rivera and Hay 2000), diet diversification (Westoby 1978, Thompson and Colgan 1990), abandonment for areas with greater potential energy density (Charnov 1976, Abrams 1984), or result in starvation and population decline. In contrast, increased

predation risk on consumers can result in movement to more protective habitats (Stein and Magnuson 1976), reduced foraging distances (Dill and Fraser 1984), or reduced food intake (Maiorana 1976, Power 1984). These forces shape consumer foraging behavior and habitat selection and typically generate a fundamental trade-off between food and protection (Sih 1980, Brown 1999). Sea otter use of more highly restricted habitats in the Aleutians is likely primarily driven by one of these forces.

If changes in prey availability or quality are currently causing sea otters to occupy restricted habitats, current habitat selection would correspond with the most abundant or energy rich prey. Habitat shifts due to prey overexploitation have been described for numerous species including kittiwake predation of sandeels (Frederiksen et al. 2005), piscivorous perch predation of roach (Persson and Eklov 1995), and zooplankton predation of hemipterans (Murdoch et al. 1984). Increases in prey patchiness can affect predator searching efficiency and realized encounter rates with prey and result in restricted habitat use (Salt 1974, Possingham 1989). Ultimately, prey depletion can limit predator population expansion when foraging habitat availability is limited (Sih 1982, Murdoch et al. 1985). The nutritional limitation hypothesis proposes that marine mammal populations (including sea otters) in the Aleutians have declined because of a reduction in overall prey abundance or a change in the relative abundance of prey of differing nutritional quality (Alverson 1992, Trites and Donnelly 2003). Primary evidence for nutritional stress involves Steller sea lions (*Eumetopias jubatus*) in the Aleutians and concomitant changes in fish stocks in the Gulf of Alaska and the Bering Sea (Merrick et al. 1997, Trites et al. 1999). A shift in the composition of available prey from high quality

forage fish to low quality gadids and flatfish resulted in a nutritionally inferior prey source and has led to the nutritional limitation of sea lions ("the junk food hypothesis"; Alverson 1992, Rosen and Trites 2000). This hypothesis is supported by studies of captive Steller sea lions that lost an average of 6.5% of their initial body mass and did not increase their food intake to compensate for the low energy they were receiving when fed low quality pollock diets (Rosen and Trites 2000, DeMaster and Atkinson 2002). Corroborative evidence for bottom-up forcing is lacking in seabird populations, which use the same prey but have not experienced similar nutritional limitation (Dragoo et al. 2007). In the current urchin barren dominated state, nearshore habitats in the Aleutians support populations of crustaceans, bivalves, gastropods, and sea urchins (Simenstad et al. 1978, Estes et al. 2010, this thesis Chapter 3). Although comparable information on sea otter prey quality during the time of the decline is not available, increases in sea urchin biomass at one Aleutian Island were recorded over the course of the sea otter decline (Estes et al. 1998). However, it has been argued that because sea otters have a diverse diet (Estes et al. 2003), increases in sea urchin biomass alone do not provide sufficient evidence against nutrition limitation (Kuker and Barrett-Lennard 2010, but see Chapter 3). Although evidence for increasing body condition and lack of age-dependent mortality patterns (i.e., those typical of food-limited populations) have been documented among sea otters captured in the Aleutians pre- and post-decline (Laidre et al. 2006), the potential relationship between prey and sea otter use of more highly restricted habitats during this same time period remains to be tested.

If predation pressure by killer whales is currently causing sea otters to occupy restricted habitats in the Aleutians, current habitat selection would reflect the use of the most highly protected habitats. Evidence suggests that killer whales caused the decline (Estes et al. 1998) and hence may also be influencing current sea otter habitat selection. Occupying habitats that provided protection from killer whale predation lessened population mortality rates during the height of the sea otter decline (Estes et al. 1998). Sea otters inhabiting a highly protected lagoon had a significantly lower rate of decline than otters in a nearby open bay, a finding attributed to the lagoon's inaccessibility to killer whales (Estes et al. 1998). Predation pressure has been recognized as a strong selective force in many prey species (Lima and Dill 1990, Deecke et al. 2002) and numerous examples of predator-mediated habitat use involving killer whales have been described. Dusky dolphins (*Lagenorhynchus obscurus*) use extremely shallow waters when within 1 km of killer whales, a behavior that possibly hides them from the predator's echolocation and reduces the killer whales' ability to maneuver (Würsig and Würsig 1980). When in proximity to killer whales during their migration, southern right whales (*Eubalaena australis*) select shallow bays and coastlines with large rocky benthic debris over smoother and deeper sandy or pebble bottoms (Sironi et al. 2004). Similar predator-mediated habitat use has been observed in bison (*Bison bison*) that preferentially forage in dense willow stands where they are less visible to wolves (*Canis lupus*) and more able to escape them (Ripple and Beschta 2006). The selective use of more highly complex habitats when in proximity to predators enables prey to escape (Sih 1980). The extent and availability of suitable escape terrain can limit prey dispersion and determine

prey home range size (Fairbanks et al. 1987, Heithaus and Dill 2006). Also, increasing distance from escape terrain is closely linked with increased prey mortality rates (Fox et al. 1992, Schroeder et al. 2010).

Evidence for predator-mediated habitat selection by sea otters, however, has been questioned. It has been suggested that sea otter use of sheltered inlets and protected coastlines is driven by the need for protection during storms (Kuker and Barrett-Lennard 2010). Coastal habitats in the Aleutians vary between steep, exposed coastlines to rocky headlands and inner bays (McNab and Avers 1996). Sea otters are known to prefer sheltered areas during rough weather (Kenyon 1969, Rotterman and Simon-Jackson 1988), generally occupying waters <40 m deep and within 400 m of the shoreline (Burn et al. 2003). It is suggested that given the frequency of storms in the Aleutians, habitats that provide shelter from storms and are prey rich are optimal and therefore expected to be the first areas occupied by expanding sea otter populations and the last areas inhabited by populations that have stabilized at low densities (Kuker and Barrett-Lennard 2010). Whether restricted habitats are being used for storm or predator protection remains to be tested. The present study took place in the Bay of Islands, Adak, in the central Aleutians. Synoptic weather patterns indicate that prevailing storm patterns affecting the Bay of Islands are westerly/northwesterly (Fett et al. 1993). If the current use of restricted habitats is driven by protection from storms, the selection of preferred habitats should include inner bay locations sheltered from prevailing weather patterns and exclude exposed outer bay locations. Conversely, if current habitat selection is driven by predator

avoidance, the location of a habitat will be less important than its three-dimensional complexity and general function as escape terrain (Sih 1980, Pfitsch and Bliss 1985).

The goal of this study was to examine currently used and historically used sea otter foraging habitats in the Aleutians to determine if their recent restricted habitat use can be attributed to nutritional limitation, predator avoidance, or the need for protection from storms. Given what is known about sea otter prey availability and coastal habitats in the Aleutians, three alternative hypotheses were articulated: (1) currently used sea otter foraging habitats will provide greater prey availability and/or prey quality than historically used habitats, (2) currently used sea otter foraging habitats will provide greater structural complexity (i.e., protection from predators) than historically used habitats, and (3) currently used foraging sites will provide greater protection from prevailing weather. To test these hypotheses, sea otter prey abundance, biomass, potential energy density, habitat structural complexity, and site exposure were quantified and compared between currently used and historically used sea otter foraging locations.

Methods

This study was conducted in nearshore habitats in the inner bay (51° 48' 19N, 176° 47' 53W) and surrounding headlands of the Bay of Islands, Adak, Alaska (Fig. 1). To determine if the differences in current and historical sea otter foraging site selection could be attributed to differences in prey availability, prey quality, habitat complexity, or storm avoidance, this study utilized a Design I study for evaluating resource selection (Manly et

al. 2002). A total of 22 sites were sampled, 11 currently used and 11 historically used sea otter foraging locations (Fig 1). Currently used sites were selected from a database of known foraging locations recorded during an intensive shore and boat-based focal observation study conducted in July and August 2008 (Fig. 1A, Estes and Tinker, unpubl. data). Historically used foraging sites, areas where otters have not been observed since 2005 but where otters were regularly seen in the early 1990's, were selected randomly from island-wide skiff survey data (Fig. 1B, Estes and Tinker, unpubl. data). Sites were located in both in inner and outer bay locations.

To determine if currently used sea otter foraging locations provide comparable prey abundance and size to historical foraging areas, sea otter prey species were sampled at each site using diver visual surveys in July 2010. Invertebrate prey were evaluated using three 20 m transects and fish prey were evaluated using one 50 m x 2 m x 2 m transect, randomly placed at each site. The target depth contour was 5-15 m based on mean sea otter foraging depths (Bodkin et al. 2004) and the observation that sea otter prey distribution patterns in the Aleutians are generally similar across this depth range (Estes et al. 2009). Invertebrate prey were sampled using three 0.25 m^2 quadrats randomly placed along each transect (n = 9 quadrats per site), inside which all potential invertebrate prey were counted, identified to species, and measured to the nearest millimeter using a 400 mm underwater ruler (test or shell maximum linear length). Fish observed along the fish sampling transect were counted, identified to species, and their length estimated to the nearest centimeter.

In addition to count and size measurements within quadrats, a subsample of sea urchins (n = 10 per site) and other invertebrate prey species (n = 3 per species per site due to lower abundances) were collected from quadrats (ADFG Permit No. CF-10-072). Only the largest individuals of each species occurring within quadrats were collected to simulate size selective foraging behavior exhibited by sea otters (Ostfeld 1982, Estes and Duggins 1995). Fish (n = 3 per species per historically used and currently used sites) were collected by divers using baited hook and line (Freiwald et al. 2009, IACUC 163475-2). Biomass per unit area (g WM·0.25 m^{-2}) was calculated using species-specific size to biomass conversion factors (Dean et al. 2002, Oftedal et al. 2007) and calibrated using size to biomass values from specimens collected in this study (test- or shell-free wet weight for invertebrates and whole wet weight for fishes).

To determine if currently used sea otter foraging locations provide comparable potential energy density to historically used sites, the caloric values of sea otter prey species were analyzed using bomb calorimetry. In preparation for ash weighing and caloric content analysis, a subsample of test- and shell-free wet samples from collected invertebrate prey and a muscle tissue subsample (1 g of pectoral muscle) from collected fish prey (n = 3 per species per historically used and currently used sites) were oven dried at 110°C for 24 h and finely pulverized into powder. Ashing was carried out in a muffle furnace at 500°C for 4 h. Weight loss from ashing was regarded as organic content and used to express the caloric content in terms of ash-free dry weight (AFDW). Homogeneous dry samples were formed into pellets and calorimetric determinations were made with both a Parr model 6200 Isoperibol bomb calorimeter with an 1108 oxygen

bomb and 6510 water handling system. Energy from dry matter ($cal \cdot g^{-1}$ DM) was then multiplied by the proportion of dry matter in the wet mass to express energy density in terms of wet mass ($kcal \cdot g^{-1}$ WM). Potential prey energy density per unit area ($kcal \cdot g^{-1}$ WM$\cdot 0.25\ m^{-2}$) was calculated using species-specific biomass to energy density conversion factors (Dean et al. 2002, Oftedal et al. 2007) and calibrated using values from specimens collected in this study. Although wet mass is influenced by ash and water dilution, it is a better representation of the actual prey biomass as consumed by sea otters (Oftedal et al. 2007).

To determine if the selection of currently used sea otter foraging sites can be attributed to differences in habitat complexity, multiple approaches were used to quantify structural complexity at currently used and historically used locations. Two scales of habitat complexity were sampled. On a large scale (ca. 20,000 m^2), coastal habitat features that increase the three-dimensional complexity of the foraging area (e.g., pinnacles, islands, and shallow boulders) were quantified. Although it is unknown which physical habitat features prevent killer whale predation on sea otters, it is thought that increasingly complex depth profiles (e.g., increased variability in depth) and increases in the size and number of pinnacles may inhibit killer whale movement and hence the probability of predation (C. Matkin pers. comm.). On the small scale (220 m^2), structural habitat features relevant to prey distribution (e.g., substrate size and relief) were quantified. Large-scale measures of habitat complexity included (1) water depth variation, (2) percent cover of persistently exposed rock pinnacles, and (3) the number of pinnacles per unit area. To measure depth variation, a hand held depth sounder recorded

depth at 5 m x 5 m grid intervals across the foraging site. Sampling grids 9 x 5 cells in size were oriented parallel to shore and were traced at the surface using a skiff and GPS track-line functions (Garmin Navigational Chart Plotter 541s). A depth measurement was recorded at each grid intersection point (n = 45 per site) enabling currently used (n = 11) and historically used (n = 11) site bathymetries to be compared as spatially explicit three-dimensional surfaces. Percent cover of exposed rock per site was estimated by a track-line tracing the periphery of the entire site and all persistently exposed rock outcrops occurring within the site (e.g., habitat features that remain above water-line throughout the tidal cycle). The areal dimension of a site and the areal extent of exposed rock within the site were calculated using geographic information systems software (ArcGIS10). In addition to estimating the percent cover of exposed rock, the number of independent pinnacles that occurred within a site was counted and is presented as pinnacles per unit area. Both attributes are important to the relative provision of refugia due to the functional differences between a site characterized by a high percent cover of exposed rock and small number of pinnacles per unit area (e.g., a single large exposed island) vs. a site characterized by a high percent cover of exposed rock and a large number of pinnacles per unit area (e.g., a field of rock spires and surge channels).

On the small scale, benthic habitat complexity was quantified by measuring (1) benthic rugosity and (2) the dominant grain size at the site. Sampling at this scale was done to quantify habitat features relevant to invertebrate and fish abundance as have been described in numerous studies (Marliave 1977, Sebens 1991, Daly and Konar 2008). Benthic rugosity was estimated at three random locations on each invertebrate and fish

transect (n = 12 per site) using the bar and chain method (McCormick 1994). This method assigns a numerical value to rugosity by measuring the difference between the actual line length between two points, designated by a rigid 1 m bar, and the observed line length between the same two points, determined using a 3 m chain laid out along the irregular seafloor bathymetry. Homogeneous mud flats tend to have rugosity ratios of 1 whereas heterogeneous boulder fields have ratios significantly greater than 1 (McCormick 1994). Rugosity values are presented as mean ± SD for each site. Dominant grain size was estimated *in situ* using a 400 mm ruler. Individual grains (n = 3) were measured at three random locations on each invertebrate and fish transect (n = 36 per site). Grain size values are presented as a mean ± SD for each site and were binned for multivariate analyses as gravel, cobble, boulder, or bedrock using a modified Wentworth scale.

To determine if the selection of restricted habitats can be attributed to protection from storms, the relative location and aspect of currently used and historically used sea otter foraging sites were related to dominant weather patterns affecting Bay of Islands, in northwestern Adak (Fett et al. 1993). Foraging site exposure to prevailing westerly/northwesterly weather was determined using compass bearing functions in geographic information systems software (ArcGIS10). Sites with ≥ 50% of the area exposed to westerly/northwesterly directions were considered exposed sites. All inner bay locations and southern/southeastern aspects in outer bay locations were considered protected from storms in the Bay of Islands.

Data Analysis - Differences in the abundance, biomass, and energy density of prey species among sites were examined with ANOVA with p-values ≤ 0.05 considered significant in all tests. In analyses of variance, sites were replicates (e.g., currently used and historically used). Differences in invertebrate and fish prey size were examined using paired *t*-tests of mean prey sizes from currently used and historically used sites with p-values ≤ 0.05 considered significant. Similarity analysis and multidimensional scaling (MDS) were used to determine if current sea otter use was attributable to prey availability (abundance, size, and biomass) or prey quality (potential energy density per individual prey and per unit area; PRIMER-E v.6, Clarke and Warwick 2001, Clarke and Gorley 2006). Prior to analyses, data were square root transformed to reduce the dominant contributions of abundant species and a similarity matrix of all samples was produced using a Bray–Curtis index. The similarity between currently used and historically used sea otter foraging sites in terms of prey abundance, biomass, and potential energy density per unit area was visualized using MDS. Similarity percentages analysis (SIMPER) was used to determine which of the above variables contributed most to the observed similarity between currently used and historically used locations. The similarity between inner and outer bay locations in terms of prey characteristics and habitat complexity measures were examined using analysis of similarity (ANOSIM) and were visualized using MDS. The variation in depth between foraging sites was calculated by finding the sample variance from depths recorded in the 5 x 9 grids (n = 45 depths) from each current (n = 11) and each historic (n = 11) location. Sample variances were log-transformed and a one-sided *t*-test was used to determine if mean variability between currently used and

historically used sites was significantly different at p-values ≤ 0.05. Three-dimensional surface plots of the sample variance in depth recorded at each spatially explicit grid cell (n = 11 sample variances for each of the 45 cells) were created to graphically compare the variance in depth at currently used and historically used sites. Binary classification was used to classify sites as refuge from prevailing storms or exposed to storms based on site location and aspect and are presented as a percent of the total sites sampled.

Results

Invertebrate sea otter prey species found during the surveys included the urchin *Strongylocentrotus polyacanthus*, the mussel *Mytilus trossulus*, the rock jingle *Pododesmus macrochisma*, chitons (*Tonicella spp.* and *Katharina tunicata*), gastropod mollusks (*Nucella ostrina, Cryptonatica aleutica*, and *Neptunea heros*) and crabs (*Pugettia producta*, *Hyas lyratus*, *Paralithodes camtschaticus*, *Phyllolithodes papillosus,* and *Pagurus ochotensis*). Fish species sampled in this study included rock greenling (*Hexagrammos lagocephalus*), kelp greenling (*H. decagrammus*), dusky rockfish (*Sebastes ciliatus*), yellow Irish lord (*Hemilepidotus jordani*), red Irish lord (*H. hemilepidotus*), rock sole (*Lepidopsetta polyxystra*), Alaskan ronquil (*Bathymaster caeruleofasciatus*), buffalo sculpin (*Enophrys bison*), and spiny lumpsucker (*Eumicrotremus orbis*).

Prey Characteristics - There was no statistical difference in prey abundance between currently used (30.8 ± 13.7 ind·m^{-2}) and historically used (35.5 ± 12.4 ind·m^{-2}) sea otter foraging sites (ANOVA, n = 22, F = 0.71, p = 0.41; Table 1). Although overall abundances were comparable, slight differences in species assemblages were noted between inner bay (protected) and outer bay (exposed) habitats, however differences were not significant (ANOVA, n = 22, F = 1.88, p = 0.73). Inner bay prey assemblages were dominated by *Strongylocentrotus polyacanthus*, followed by gastropods, chitons, and crabs. Outer bay prey assemblages were also dominated by *S. polyacanthus*; however, the next most common species were *Pododesmus macrochisma*, *Mytilus trossulus*, and gastropods. Crabs were patchy in abundance and were represented primarily by individual *Paralithodes rathbuni* and *Phyllolithodes papillosus*. Fish species occurred in low abundances in both inner and outer bay locations and no significant difference between fish abundances in currently used (0.05 ± 0.05 ind·m^{-2}) and historically used locations (0.07 ± 0.06 ind·m^{-2}) were detected (ANOVA, n = 22, F = 0.68, p = 0.34). The most common fish species in the inner bay were *Hexagrammos decagrammus*, *Lepidopsetta polyxystra* and *Bathymaster caeruleofasciatus* and in the outer bay were *H. decagrammus*, *Hemilepidotus jordani* and *B. caeruleofasciatus*, however differences were not significant (ANOVA, n = 22, F = 0.91, p = 0.51). Although no large schools of Atka mackerel, *Pleurogrammus monopterygius*, were recorded during fish surveys conducted in this study, several massive schools were observed at outer bay locations during tidal exchanges as has been noted elsewhere in this region (Anthony et al. 2008).

There was no statistical difference in available prey biomass between currently used (707.8 ± 337.1 $g \cdot m^{-2}$) and historically used (828.2 ± 329.2 $g \cdot m^{-2}$) sea otter foraging sites (ANOVA, n = 22, F = 0.84, p = 0.31; Table 2). *Strongylocentrotus polyacanthus* contributed the greatest available biomass per unit area (29.35 ± 10.3 $g \cdot m^{-2}$) followed by gastropods in the inner bay (2.3 ± 0.3 g m^{-2}) and *Pododesmus macrochisma* in the outer bay (2.9 ± 1.1 $g \cdot m^{-2}$).

There was no statistical difference in potential energy density per unit area between currently used (393.7 ± 149.1 $kcal \cdot g^{-1}$ $0.25 \cdot m^{-2}$) and historically used (441.3 ± 154.9 $kcal \cdot g^{1} \cdot 0.25$ m^{-2}) sea otter foraging sites (ANOVA, n = 22, F = 0.54, p = 0.47; Table 3). The highest potential energy density prey sampled in this study were fish (1.38 ± 0.08 $kcal \cdot g^{-1}$ WM) followed by *Pododesmus macrochisma* (0.86 ± 0.04 $kcal \cdot g^{-1}$ WM) and crabs (0.69 ± 0.23 $kcal \cdot g^{-1}$ WM). No significant differences in potential prey density between inner and outer bay were detected (ANOVA, n = 22, F = 0.74, p = 0.53). Due to low abundances and comparable energy density per unit of tissue, individual fish species were grouped for all biomass and potential energy density comparisons.

No significant differences in prey size were detected for any invertebrate ($t(22)$ = 0.86, p = 0.43) or fish ($t(22)$ = 1.06, p = 0.33) prey species between currently used and historically used foraging areas (Fig. 2). No significant differences were detected in prey size between inner and outer bay locations (ANOVA, n = 22, F = 2.02, p = 0.33). Although there were a greater number of large sea urchins at historically used foraging areas in relation to currently used foraging areas, no significant differences between urchin standing stock biomass were detected (ANOVA, n = 22, F = 1.39, p = 0.27).

Currently used and historically used sea otter foraging locations did not show a clear separation in terms of relative prey abundance, size, biomass, and energy density using multidimensional scaling analyses (MDS; Fig. 3). Available prey biomass (SIMPER 11%) and potential energy density (SIMPER 13%) did not contribute to the dissimilarity between current and historic foraging sites, as indicated by similarity percentages analyses. Currently used and historically used sites did not show a clear separation based on their location in inner bay or outer bay habitats in terms of prey abundance, size, biomass, and energy density (MDS; Fig. 4).

Habitat Complexity - Depth was significantly more variable at currently used sites ($\sigma^2 = 1.92 \pm 0.1$) than at historically used sites ($\sigma^2 = 1.62 \pm 0.1$), as indicated by a *t*-test of sample variances from each location ($t(20) = 8.33$, $p < 0.0001$). Spatially explicit surface plots of sample variances from each grid cell from currently used sites exhibited greater variation in depth than grid cells at historical sites (Fig. 5). Currently used sites had significantly more exposed rock (ANOVA, $n = 22$, $F = 55.4$, $p < 0.001$) and more pinnacles per unit area (ANOVA, $n = 22$, $F = 26.3$, $p < 0.001$) than historical sites (Table 2). In contrast to larger scale comparisons, smaller scale comparisons did not reveal significant differences between locations. Benthic rugosity and grain size were comparable between currently used and historically used sites (Table 2). Sediment composition varied widely across the study area, from cobble in inner bays to large stable boulders or continuous bedrock in both inner and outer bay sites. As expected, minimum grain sizes were generally larger in outer bay (boulder) compared to inner bay (cobble)

locations. The separation in sites based on their inner or outer bay location was significant (ANOSIM, R = 0.876) and was driven by variation in depth, percent exposed rock, and number of pinnacles per unit area (SIMPER, 91%).

Storm Avoidance - Currently used foraging areas do not provide protection from storms based on dominantly westerly/northwesterly prevailing weather conditions in the Bay of Islands. Of the 22 sites sampled in this study, 13 sites were located in the inner bay (four currently used and nine historically used sites) and nine sites were located in the outer bay (seven currently used and two historically used sites). Only two currently used sites were located in the inner bay with eastern/southeastern aspects. Of the outer bay locations, only one currently used site was situated with a southeasterly aspect; however, it should be noted that this site experiences extremely high currents during regular tidal exchanges (Fett et al. 1993). These observations support the theory that the separation of currently used and historically used sites is not based on protection from storms (Fig. 6).

Discussion

The current use of restricted habitats by sea otters in the Bay of Islands, Adak Alaska cannot be attributed to prey depletion, changes in prey quality, or the need for protection from storms. Sea otter prey were equally abundant and provided similar biomass and potential energy density at both historically and currently used sea otter foraging locations. Sea otter foraging locations did, however, differ significantly in terms

of their large-scale structural complexity. Currently used locations were characterized by greater variability in seafloor bathymetry, greater percent exposed rock, and more pinnacles per unit area. In contrast, historically used locations were generally broad open coastlines with little bathymetric relief and little or no exposed rock or coastal structure. These findings suggest that the recent shift from historical to current foraging locations by sea otters inhabiting the Bay of Islands was not driven by changes in prey quality or protection from storms. It is suggested that the current use of more highly complex habitat is predator-mediated and that post-decline habitat selection is based on predator avoidance.

Analyses of prey communities at historically used and currently used locations do not provide evidence for restricted habitat use based on differences in prey abundance or prey quality. Sea urchins, the preferred sea otter prey in the Aleutians (Estes and Palmisano 1974) were the most abundant prey in the study area and were consistently dense regardless of sea otter use, variation in large- or small-scale habitat complexity, or foraging site location. The nutritional limitation of sea otters would require changes in the abundance of key prey species ("acute nutritional stress"; Trites and Donnelly 2003). Given the abundance and uniform prey availability in the Bay of Islands, it is unlikely that sea otters could feasibly be limited by acute nutritional stress in the two decades since the population decline. Prey overexploitation, an additional cause of acute nutritional stress, can also be ruled out given overall increases in sea urchin abundance at Adak Island during the sea otter decline (Estes et al. 1998). Prey depletion through size selective predation by sea otters would predictably lead to size limited prey populations

(Estes and Palmisano 1974, Bodkin et al. 2001, Laidre and Jameson 2006); however, no differences in prey size or biomass were detected between historically used and currently used sites in this study.

The comparable quality of prey resources available to sea otters at historically and currently used sea otter locations discredits the hypothesis that sea otter shifted to a more highly restricted habitat because of diminished prey quality. Changes in prey quality ("chronic nutritional stress"; Trites and Donnelly 2003) in the nearshore Aleutians are an unlikely cause of restricted habitat use given the stability of the dominant nearshore community for the past two decades. The sea otter population decline triggered a phase shift from a kelp dominated to an urchin-dominated community during the 1990's (Estes et al. 1998, Estes et al. 2005). As a result, the nearshore system is dominated by urchins and largely devoid of kelp (Estes and Palmisano 1974, Simenstad et al. 1978). Although the lack of kelp does affect benthic productivity (Duggins et al. 1990) and urchin barrens are generally associated with poor nutritional resources (Harrold and Reed 1985), the shift to an urchin dominated system, in itself, was not enough to nutritionally compromise sea otters nor does it explain their current use of restricted habitats (but see Chapter 3). The uniform potential energy density of numerous prey species at both historically and currently used foraging areas provides strong evidence against chronic nutritional stress.

The principal difference between currently and historically used sea otter foraging locations is structural complexity. Currently used locations were typically associated with rocky and irregular coastlines that divided large portions of the available foraging habitat

into channels and pinnacles. In contrast, historically used foraging locations were typically associated with broad open coastlines, gradual seafloor relief and very few or no pinnacles. The shift to more highly protective habitats is often predator-mediated and can have significant effects on prey habitat use (Stein and Magnuson 1976, Sih 1982). The movement to more protected habitats often entails the increased use of escape terrain (Sih 1980). The definition of escape terrain varies according to the predator-prey relationship. For example, under intense predation-risk bighorn sheep preferred rock outcrops and avoided open grasslands. In this case optimal escape terrain was defined by proximity to cliffs and low visibility to predators (Fairbanks et al. 1987). Similar habitat selection criteria were displayed by ibex (*Capra ibex)* under predation pressure from snow leopards (*Panthera uncia*) in the Himalaya. In this case 4,000-4,800 m elevation, slopes averaging 31° and deep snowpack constituted viable escape terrain (Fox et al. 1992). For sea otters, and marine mammals in general, the concept of escape terrain is less well defined. The structural similarities within currently used foraging locations sampled in this study suggest that highly variable seafloor bathymetry, 13 - 28% exposed rock and roughly 10 - 28 pinnacles per 20,000 m^2 are suitable escape terrain. There are several critical assumptions in assessing currently used sea otter foraging habitats as escape terrain including (1) that predators continue to affect sea otters in this area, (2) that sea otters that once associated with historical locations have either moved to current locations or were killed, and (3) that remaining sea otters have successfully avoided predation by associating with these current locations.

The alternative explanation for the use of more highly protective habitats as refuge from storms (Kuker and Barrett-Lennard 2010) can be disregarded because currently used sites are predominantly exposed rocky headlands or the outer coasts of islands. These areas are directly exposed to the prevailing weather patterns impacting the Bay of Islands within northwestern Adak. The sites of greatest storm protection in the study area are in the inner bay or are situated at aspects where few sea otters are currently found.

In contrast to the marked differences in large-scale habitat complexity between historically used and currently used foraging locations, no significant differences were detected at smaller habitat complexity scales. Benthic invertebrates and epibenthic fishes respond to changes in substrates and tend to vary in abundance, composition, and size with varying three-dimensional structure (Hovel and Romuald 2001, Hamilton and Konar 2007). Available prey species in this study were relatively uniform in their availability regardless of sea otter use or general location in the bay. This is likely due to the comparable distribution of grain sizes and rugosity values at historical and currently used foraging sites. In the absence of predators and with the uniform availability of prey resources, it is predicted that animals have perfect information about the distributions of predators and resources and can freely move to the habitat where their fitness gains will be highest ("ideal free distribution"; Fretwell 1972). Consequently, animals should distribute themselves such that the proportion of individuals in each habitat matches the proportion of resources available there. Restricted habitat use patterns in this study, however, do not match the even distribution of prey resources. Deviations from ideal free

distribution were observed in guppies when fish predators were added to foraging patches with evenly distributed guppy prey (Abrahams and Dill 1989). The use of more highly restricted habitats by sea otters, despite evenly distributed prey resources, likely reflects a similar response to increased predation pressure.

If killer whale predation is mediating sea otter habitat selection in the Bay of Islands, sea otter prey availability is likely to change over time due to overexploitation (Brown et al. 1999). Intense predation pressure can generate a fundamental trade-off between food and protection, forcing prey species to balance habitat selection between safe and productive locations (Sih 1980; Brown 1999). Sea otters preferentially select the largest and most calorically rich prey first before switching to smaller and less valuable prey (Ostfeld 1982, Garshelis 1983). Depending on prey choices associated with restricted habitats and the mobility of sea otters under the risk of predation, prey depletion and nutritional stress are potential threats to long-term associations with restricted habitats. In the case of alpine ungulates, high-altitude cliffs are a safe habitat because they are less commonly used by predators and ungulates can escape them there (Festa-Bianchet 1988, Gross et al. 1996). Because of these advantages, areas close to escape terrain are often heavily used for foraging compared to areas located farther away (Pfitsch and Bliss 1985). Since intensive grazing or browsing can greatly reduce plant abundance and quality (Cote et al. 2004, Schoenecker et al. 2004), areas near escape terrain may be less productive due to grazing stress (e.g., depleted plant nutrients and carbohydrate reserves) than farther areas. Should sea otters continue to be restricted to a

limited foraging habitat due to predation pressure from killer whales, further sea otter population decline could result from overexploitation and local prey depletion.

In conclusion, the use of restricted habitats by sea otters currently inhabiting the Bay of Islands, Adak, is not driven by prey depletion or the need for protection from storms. Restricted habitat use is likely predator mediated and has led to the selection of habitats that provide the greatest refuge from predation. This is supported by 1) currently used sea otter foraging locations providing similar prey quantity and quality to historically used habitats, 2) currently used foraging sites showing more structural complexity than historical sites, and 3) currently used foraging locations predominantly being situated in areas exposed to prevailing weather. This study directly tested the nutritional limitation hypothesis for restricted habitat use (Kuker and Barrett-Lennard 2010). Findings contradict this hypothesis and are consistent with the hypothesis that sea otter restricted habitat use is caused by increased killer whale predation (Estes et al. 1998). It is speculated that, given sea otters historical use of less structurally complex habitats, selection was not always predator mediated. Increasing predation pressure by killer whales (Estes et al. 1998) likely has resulted in the selective use of escape terrain. Due to the limited availability of suitable escape terrain from killer whale predation, sea otter habitat use is restricted. The shift to more complex habitats and the failure to return to pre-decline populations densities (Estes et al. 2005) despite available prey resources (Stewart and Konar, in press), provides further indirect evidence for the predator-mediated limitation of sea otters using restricted habitats in the Aleutians. Although effective escape terrain from killer whale predation remains to be defined for sea otters,

characteristics of restricted habitat use may pertain to other marine mammals that utilize nearshore habitats. The effective analyses of populations under potential prey availability-predator avoidance trade-offs requires corresponding analyses of prey distribution, prey quality, and predation risk.

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Table 1. Prey abundance at currently and historically used foraging locations. Invertebrate prey species include *Strongylocentrotus polyacanthus (S. polyac.)*, *Pododesmus macrochisma (P. macr.)*, *Mytilus trossulus (M. tross)*, gastropod spp. *(Nucella ostrina*, *Cryptonatica aleutica*, and *Neptunea heros)*, chiton spp. *(Tonicella spp.* and *Katharina tunicata)*, crab spp. (*Pugettia producta*, *Hyas lyratus*, *Paralithodes camtschaticus*, *Phyllolithodes papillosus,* and *Pagurus ochotensis)*, and fish spp. (*Hexagrammos lagocephalus*, *H. decagrammus*, *Sebastes ciliatus*, *Hemilepidotus jordani*, *H. hemilepidotus*, *Lepidopsetta polyxystra*, *Bathymaster caeruleofasciatus*, *Enophrys bison*, and *Eumicrotremus orbis)*. Abundance (individuals·0.25 m^{-2}) is expressed as mean ± SD at current (n = 11) and historical (n = 11) sites. No significant differences in prey abundance were detected between current and historical sites (ANOVA, $p \leq 0.05$).

	Abundance (individuals·0.25 m^{-2})					
	All sites		Inner bay		Outer bay	
	current	historic	current	historic	current	historic
Species	(n = 11)	(n = 11)	(n = 4)	(n = 4)	(n = 7)	(n = 7)
S. polyac.	27.1 ± 10.2	31.6 ± 9.7	24.2 ± 11.1	27.3 ± 9.1	31.1 ± 9.8	34.8 ± 10.1
P. macr.	2.3 ± 2.1	3.1 ± 2.2	0.7 ± 0.5	1.1 ± 0.6	2.6 ± 0.7	3.3 ± 1.1
M. tross.	1.7 ± 0.6	2.1 ± 0.7	0.9 ± 0.5	1.1 ± 0.7	2.1 ± 0.3	2.5 ± 0.5
gastr. spp.	1.9 ± 0.5	2.2 ± 0.4	2.1 ± 0.3	2.5 ± 0.3	1.7 ± 0.4	1.5 ± 0.2
chiton spp.	1.2 ± 0.3	1.4 ± 0.4	1.6 ± 0.2	1.9 ± 0.3	0.9 ± 0.1	0.7 ± 0.2
crab spp.	1.2 ± 1.1	1.5 ± 1.3	1.3 ± 1.1	1.6 ± 1.4	1.1 ± 1.0	1.4 ± 0.9
fish spp.	0.05 ± 0.05	0.07 ± 0.06	0.02 ± 0.03	0.04 ± 0.04	0.06 ± 0.05	0.07 ± 0.05

Table 2. Prey biomass at currently and historically used foraging locations. Invertebrate prey species include *Strongylocentrotus polyacanthus (S. poly.)*, *Pododesmus macrochisma (P. mac.)*, *Mytilus trossulus (M. tros)*, gastropod spp. *(Nucella ostrina*, *Cryptonatica aleutica*, and *Neptunea heros)*, chiton spp. *(Tonicella spp.* and *Katharina tunicata)*, crab spp. (*Pugettia producta*, *Hyas lyratus*, *Paralithodes camtschaticus*, *Phyllolithodes papillosus,* and *Pagurus ochotensis)*, and fish spp (*Hexagrammos lagocephalus*, *H. decagrammus*, *Sebastes ciliatus*, *Hemilepidotus jordani*, *H. hemilepidotus*, *Lepidopsetta polyxystra*, *Bathymaster caeruleofasciatus*, *Enophrys bison*, and *Eumicrotremus orbis)*.Biomass (g wet mass·0.25 m^{-2}) is expressed as mean ± SD at current (n = 11) and historical (n = 11) sites. No significant differences in prey abundance were detected between current and historical sites (ANOVA, $p \leq 0.05$).

	Biomass (g wet mass·0.25 m^{-2})					
	All sites		Inner bay		Outer bay	
	current	historic	current	historic	current	historic
Species	(n = 11)	(n = 11)	(n = 4)	(n = 4)	(n = 7)	(n = 7)
S. poly.	542.3 ± 204.1	632.2 ± 194.2	484.7 ± 221.5	546.4 ± 183.4	622.2 ± 196.3	696.7 ± 203.8
P. mac.	86.3 ± 78.7	116.2 ± 82.5	26.3 ± 18.7	41.3 ± 22.5	97.5 ± 26.3	123.7 ± 41.2
M. tros	19.7 ± 6.9	24.3 ± 8.1	10.4 ± 5.8	12.7 ± 8.2	24.3 ± 3.5	29.1 ± 5.7
gast. spp	56.8 ± 14.9	65.7 ± 11.9	62.7 ± 8.9	74.4 ± 7.9	50.8 ± 11.9	44.7 ± 5.9
chit. spp.	23.6 ± 5.9	27.6 ± 7.8	31.5 ± 3.9	37.4 ± 5.9	17.7 ± 1.9	13.7 ± 3.9
crab spp.	78.8 ± 71.5	97.5 ± 84.5	84.6 ± 70.7	104.1 ± 91.2	71.5 ± 64.6	91.6 ± 58.1
fish spp.	12.5 ± 12.2	17.5 ± 15.7	7.6 ± 7.5	11.9 ± 10.1	14.4 ± 12.3	16.9 ± 13.1

Table 3. Prey energy density at currently and historically used foraging locations. Invertebrate prey species include *Strongylocentrotus polyacanthus (S. polyac.)*, *Pododesmus macrochisma (P. macrochr.)*, *Mytilus trossulus (M. tross)*, gastropod spp. *(Nucella ostrina*, *Cryptonatica aleutica*, and *Neptunea heros)*, chiton spp. *(Tonicella spp.* and *Katharina tunicata)*, crab spp. (*Pugettia producta*, *Hyas lyratus*, *Paralithodes camtschaticus*, *Phyllolithodes papillosus,* and *Pagurus ochotensis)*, and fish spp (*Hexagrammos lagocephalus*, *H. decagrammus*, *Sebastes ciliatus*, *Hemilepidotus jordani*, *H. hemilepidotus*, *Lepidopsetta polyxystra*, *Bathymaster caeruleofasciatus*, *Enophrys bison*, and *Eumicrotremus orbis)*. Potential energy density (kcal·g wet mass·0.25 m^{-2}) is expressed as mean ± SD at current (n = 11) and historical (n = 11) sites. No significant differences in prey abundance were detected between current and historical sites (ANOVA, $p \leq 0.05$).

	Potential energy density (kcal g wet mass·0.25 m^{-2})					
	All sites		Inner bay		Outer bay	
	current	historic	current	historic	current	historic
Species	(n = 11)	(n = 11)	(n = 4)	(n = 4)	(n = 7)	(n = 7)
S. poly.	130.1 ± 48.9	152.7 ± 46.6	116.3 ± 53.2	131.8 ± 44.2	149.3 ± 47.1	167.2 ± 48.9
P. mac	71.6 ± 65.3	96.4 ± 68.4	21.8 ± 15.5	34.2 ± 18.6	80.9 ± 21.8	102.6 ± 34.1
M. tros	9.8 ± 3.4	12.1 ± 4.0	5.2 ± 2.9	6.4 ± 4.1	12.2 ± 1.7	14.6 ± 2.8
gast. spp.	73.8 ± 19.3	85.4 ± 15.4	81.5 ± 11.5	96.3 ± 10.2	66.3 ± 15.4	58.1 ± 7.6
chit. spp.	21.2 ± 5.3	24.8 ± 7.0	28.3 ± 3.5	33.6 ± 5.3	15.9 ± 1.7	12.3 ± 3.4
crab spp.	54.3 ± 49.3	67.3 ± 58.3	58.5 ± 48.7	71.6 ± 62.9	49.3 ± 44.5	63.2 ± 40.1
fish spp.	17.2 ± 16.8	24.1 ± 21.6	10.5 ± 10.3	16.4 ± 13.9	19.8 ± 16.9	23.3 ± 18.0

Table 4. Habitat complexity at currently and historically used foraging locations. Values are presented as mean ± SD. Significant differences (ANOVA, $p \leq 0.05$) are indicated by (*).

	Inner bay		Outer bay	
	current	historic	current	historic
Complexity	(n 4)	(n 9)	(n 7)	(n 2)
site area (m^2)	21926.7 ± 682.6	23567.2 ± 772.6	20881.1 ± 833.8	221778.2 ± 449.8
% exposed rock	13.3 ± 5.6 *	1.3 ± 3.6	28.3 ± 12.9 *	6.2 ± 5.2
pinnacles per site	9.8 ± 2.7 *	0.7 ± 1.1	27.9 ± 10.9 *	5.6 ± 2.7
benthic rugosity	2.5 ± 0.04	2.1 ± 0.07	2.8 ± 0.01	3.1 ± 0.01
grain size bin	cobble/boulder	cobble	bedrock	bedrock
grain size min. (mm)	261.1	67.5	> 1524	> 1524
grain size max. (mm)	> 1524	> 1524	> 1524	> 1524

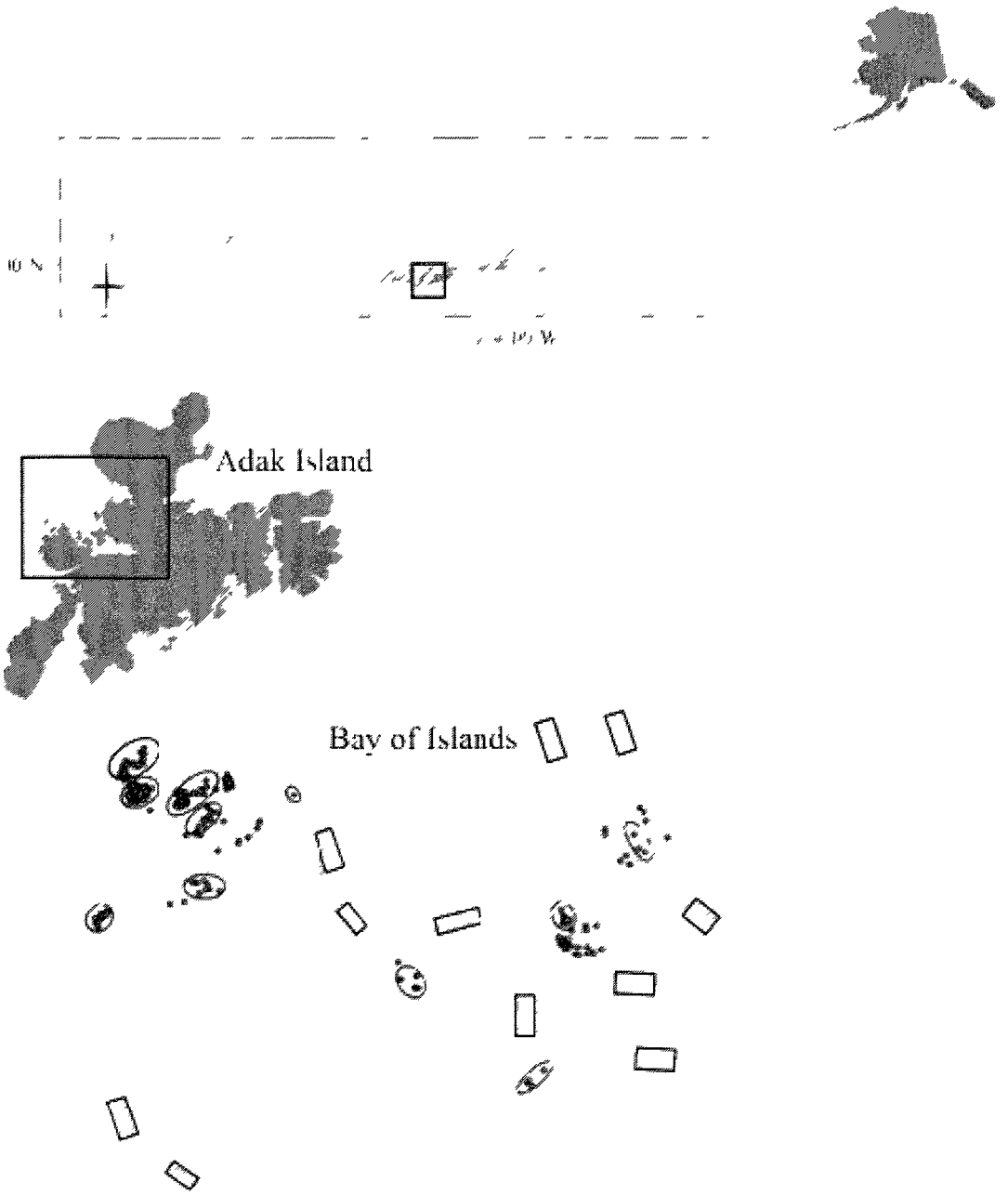

Fig 1. The study area on Adak Island, Aleutian Islands, Alaska Currently used sea otter foraging locations, indicated by open circles, were collected by focal observation during summer 2008 (n=11) Each dot indicates a site where a series of feeding dives were recorded Historically used foraging locations, indicated by open rectangles, are areas where otters were regularly seen in USGS skiff surveys in the 1970's and 1980's but have not been observed since the early 1990's (n=11) (Image courtesy of M.T Tinker)

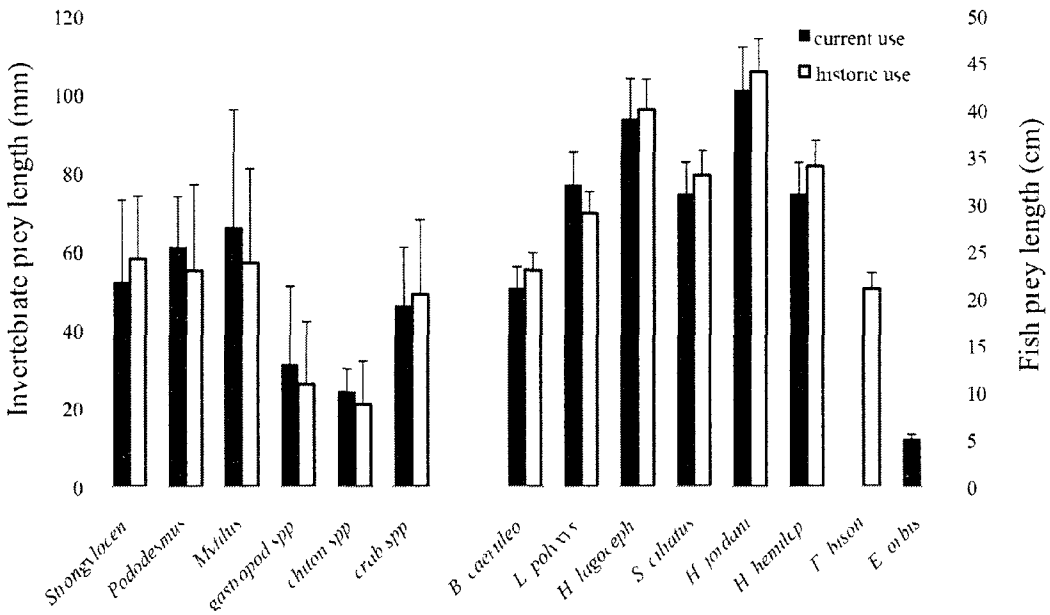

Figure 2. Sea otter prey sizes at current and historically used foraging sites. Invertebrate prey size is recorded as the maximum linear length of the test or shell (mm) and in fish prey is recorded as the total length (cm) and is expressed as mean ± SD. Invertebrate prey species include: *Strongylocentrotus polyacanthus* (n = 2938 in current, 3128 in historic), *Pododesmus macrochisma* (n = 288 in current, 307 in historic), *Mytilus trossulus* (n = 208 in current, 189 in historic), gastropod spp. (n = 198 in current, 217 in historic), chiton spp. (n = 117 in current, 138 in historic), crab spp. (n = 114 in current, 129 in historic), and fish spp. (n = 115 in current, 127 in historic) No significant differences in prey size were detected between current and historical sites for any prey species (paired *t*-test, $p < 0.05$).

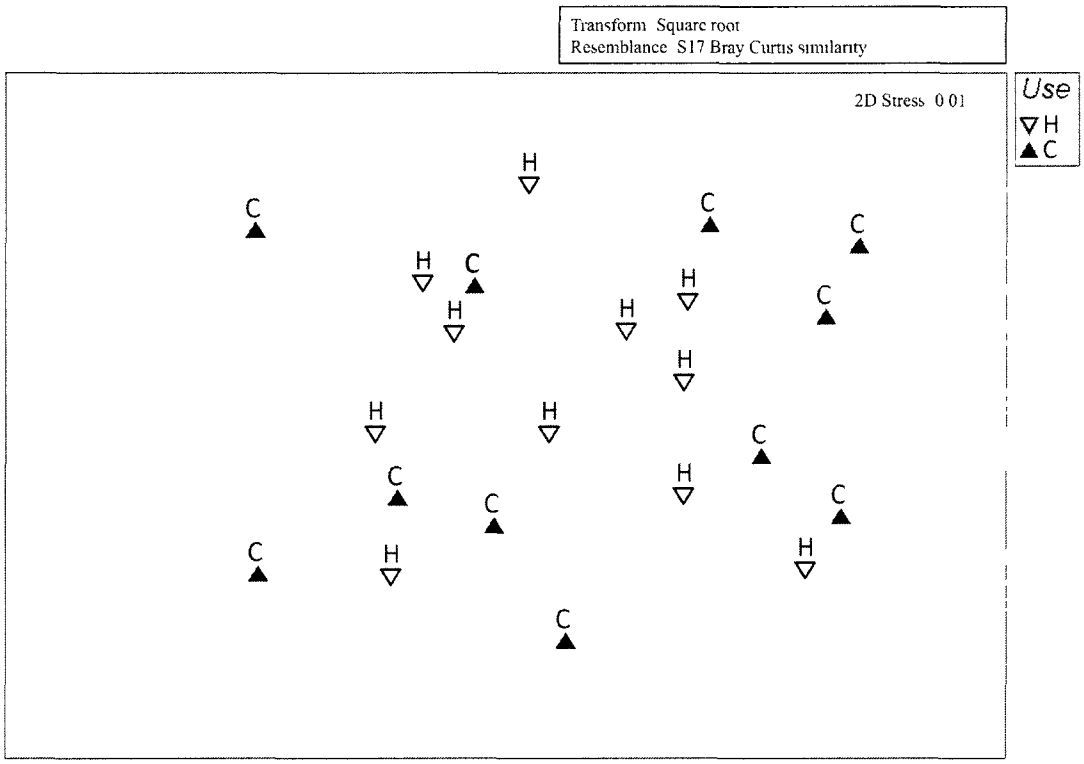

Figure 3. MDS ordination of current and historically used foraging sites. Sea otter prey size, abundance, biomass, and energy density contribute to the gradient in separation in currently used (C) and historically used (H) habitats.

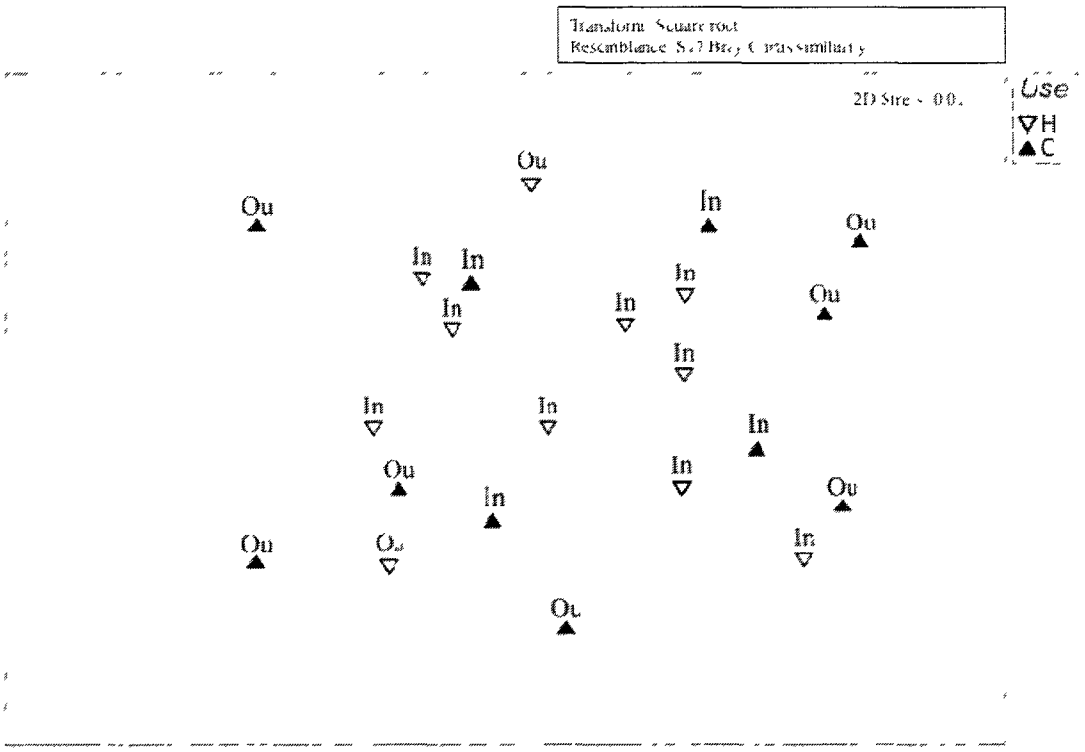

Figure 4. MDS ordination of inner and outer bay habitats. Sea otter prey size, abundance, biomass, and energy density contribute to the gradient in separation in inner bay (In) and outer (Ou) habitats.

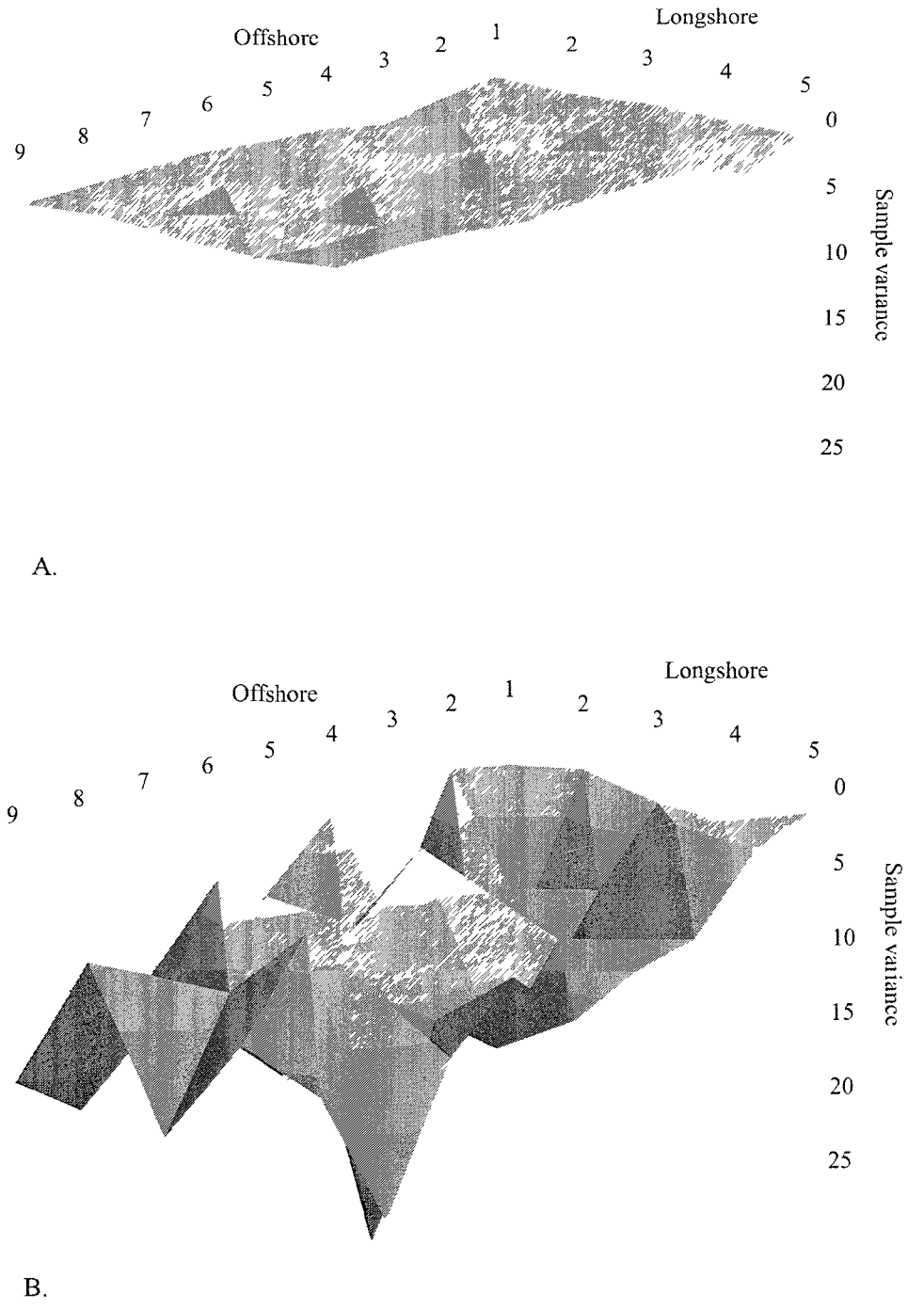

Figure 5. Variance in depth at current and historically used foraging sites. Surface plots were generated using sample variances from each spatially explicit grid coordinate (n = 45) from 11 historically used (A) and 11 currently used (B) locations.

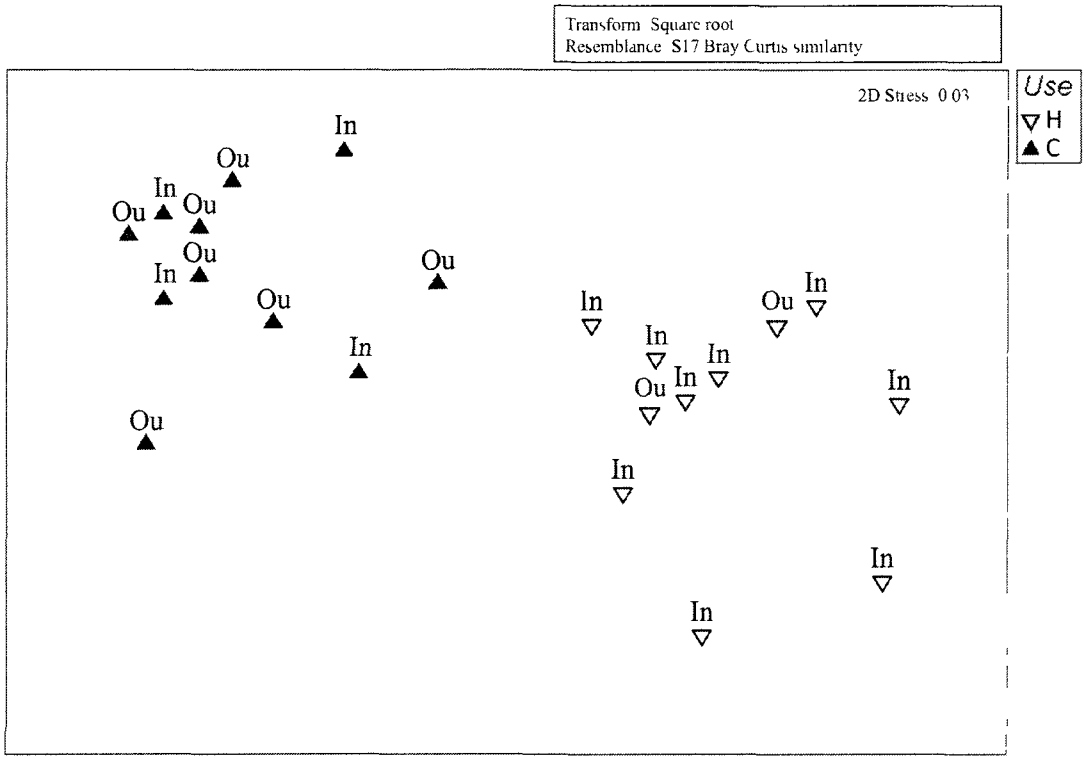

Figure 6. MDS ordination of habitat complexity of inner and outer bay habitats. Sea otter prey characteristics and structural habitat complexity measures contribute to the separation in inner (In) and outer bay (Ou) sites. Symbols indicate current sea otter foraging use (closed triangle) or historical sea otter foraging use (open triangle).

CHAPTER 5

Conclusion

Research described in this dissertation focuses on sea otter resource selection in populations inhabiting two different nearshore systems in Alaska, mixed sediment habitats in Lower Cook Inlet and bedrock habitats in the Aleutian Islands. Sea otter populations inhabiting these two systems have markedly different population status and interact with different habitat types. In the heterogeneous estuarine system in Kachemak Bay, sea otter populations increased from <1,000 individuals in the 1990's to 3,600 individuals in 2008, resulting in approximately 5.7 otters·km^{-2} inhabiting Kachemak Bay today (Gill et al. 2009). In contrast, sea otter populations in the central and western Aleutians have undergone a precipitous decline averaging about 25% per year since the 1990's (Estes et al. 1998, Doroff et al. 2003). The sea otter population in the Aleutians decreased from 118,000 individuals prior to 1990's to 8,742 individuals in 2000, resulting in approximately 1.7 otters·km^{-2} inhabiting the central and western Aleutians today (Doroff et al. 2003, Pfister and DeMaster 2006). This dissertation focused on how sea otter habitat might influence resource selection in these two coastal systems, one in which otters are increasing and one where they are decreasing. In both regions, otters are below their carrying capacity. Six habitat attributes pertinent to sea otter foraging were examined, including benthic habitat type, benthic habitat complexity, prey availability, prey quality, habitat refuge from predation, and habitat protection from storms. Findings

from this research suggest that sea otter foraging site selection is based on habitat complexity in areas with increasing populations, but in areas with high predation pressure, proximity to suitable escape terrain appears to be more important than prey quality or benthic habitat complexity.

Sea otters forage on a wide range of marine invertebrates and their diet varies by available habitat. In rocky habitats sea otters generally select epifaunal prey species including crabs, urchins, and mussels associated with increased three dimensional structure provided by cracks, crevices, and kelps. In soft sediment habitats sea otters alter their foraging strategy to exploit buried infaunal prey, including clams and worms. The current understanding of sea otter foraging behavior comes primarily from studies in rocky habitats such as those in the central and western Aleutian Islands (Estes and Palmisano 1974, Simenstad et al. 1978). In these rocky habitats, sea otters optimize their foraging efficiency by selectively feeding on the largest, most abundant, calorically rich prey first (often sea urchins) before switching to other less profitable prey species (Duggins 1980, Ostfeld 1982). This behavior is, however, highly influenced by prey availability, prey quality, the threat of predation, and the need to obtain protection from storms. In other areas, soft sediment habitats are also used extensively by sea otters, where bivalves account for the majority of their prey (Estes et al. 1981, Garshelis 1983, Kvitek and Oliver 1988). In these habitats, otters have been shown to optimize their foraging by preferentially feeding in patches containing smaller, but easily excavated prey rather than in adjacent patches containing larger, but more deeply buried individuals of the same species (Kvitek et al. 1988). Many sea otter feeding areas, like those

characteristic of Kachemak Bay in the Lower Cook Inlet, consist of a mosaic of both soft and rocky habitat types and are thus capable of supporting both types of prey assemblages and sea otter foraging strategies. Although sea otters have been shown to profoundly deplete their prey abundance in both rocky (Estes et al. 1978) and soft-bottom habitats (Garshelis 1983, Wendell et al. 1986), the influence of habitat type on sea otter foraging habitat selection remains undescribed. This dissertation examined the influence of habitat type on factors relevant to sea otter foraging site selection in both a heterogeneous system and in a rocky system where foraging sea otters are exposed to predation pressure and prevailing weather.

Research presented in Chapter 2 provides evidence for sea otter selection of rocky habitats over soft-bottom habitats despite abundant, calorically rich infaunal prey. In Kachemak Bay, sea otters foraging in heterogeneous habitats responded to fine-scale variation in sediment composition and sea floor rugosity and selectively foraged on accessible epifaunal prey and not on infaunal prey with relatively higher energy density. The use of prey resources disproportionate to their availability and potential energy density has been suggested for sea otters elsewhere in their range (VanBlaricom 1988, Kvitek et al. 1993). The preferential selection of more complex habitats has been shown in many organisms including benthic invertebrates (Sebens 1991, Daly and Konar 2008), demersal fishes (Marliave 1977, McCormick 1994, Hamilton and Konar 2007), and marine mammals (Ban and Trites 2007) and is generally attributed to proximity to prey resources (Raffaelli and Hughes 1978, Suryan and Harvey 1998). The effort required to capture prey is an important factor in predicting foraging site selection and determining

the relative profitability of prey (Pyke 1984, Stephens and Krebs 1986). The most profitable prey or prey patch are not always the most targeted due to high energetic costs associated with access and handling time. Sea otters have been shown to preferentially forage on small, shallow buried prey versus much larger, but more deeply buried individuals of the same species (Kvitek et al. 1988). Given findings from Chapter 2, it is possible that sea otters inhabiting heterogeneous environments opportunistically exploit low value prey (e.g., small and/or dispersed mussel, urchin, and crab species) during searches for high value prey (e.g. large urchins). In relation to energy-rich buried prey (e.g., large clams), the handling time required to process easily collected epifaunal species such as crabs is minimal and, therefore, very little time is lost searching for high energy prey. Consequently, the abundance of low value prey could compensate for their low value (Stephens and Krebs 1986). This foraging strategy likely serves sea otters well in environments with depleted calorically rich and easily captured prey, plentiful buried prey, and patchy epifaunal prey.

Research presented in Chapter 3 examined the effects of alternate stables states on the quality of prey available to sea otters foraging in rocky habitats of the central and western Aleutian Islands. The trophic cascade induced by sea otters in rocky ecosystems drives nearshore habitats to one of two distinctive phase states (Steneck et al. 2002), kelp forests or sea urchin barrens. Both phase states are stable equilibrium points and intermediate community configurations are not stable and not common (Estes and Duggins 1995). Kelp forests are more productive than sea urchin barrens and can fix an estimated four times more inorganic carbon per unit area through photosynthesis

(Duggins et al. 1989), which increases growth rates and population sizes of various consumer species (Duggins et al. 1989, Estes et al. 2003). For instance, the rock greenling, a common kelp forest fish in the central and western Aleutian Islands, are an order of magnitude more abundant in kelp forests than in sea urchin barrens (Reisewitz et al. 2006). In its current stable state the nearshore community in the central and western Aleutian Islands is dominated by abundant but low quality sea urchin prey. Expansive sea urchin barrens support dense sea urchin populations that are generally smaller and provide less biomass and energy density per individual than kelp forest urchins. Interspersed in the system is a patchwork mosaic of remnant kelp forests that support relatively few but large, calorically rich individuals. Given sea otter feeding rates and assimilation efficiency when foraging on urchins (Yeates et al. 2007), sea otter daily energy requirements are easily met foraging in either community. Both kelp forest and barren urchins sampled in this study were comparable to potential energy density values of individual urchins elsewhere in the sea otter range. Consequently, though changes in prey quality associated with phase shifts represent an ecosystem service loss to predators, prey quality differences are not significant enough to explain the rate of the sea otter population declines reported during the 1990's (ca. 25% per year; Estes et al. 1998), nor are they sufficient to explain the inability of the sea otter population to recover to pre-decline densities in the two decades since the decline.

Research presented in Chapter 4 directly tested the nutritional limitation, predator avoidance, and storm protection hypotheses for the current use of sea otters of restricted habitats in the Aleutians. Results suggest that the current use of restricted habitats by sea

otters in the Bay of Islands, Adak Alaska cannot be attributed to prey depletion or changes in prey quality. Sea otter prey were equally abundant and provided similar biomass and potential energy density at both historically and currently used sea otter foraging locations. Given the abundance and uniform prey availability in the Bay of Islands, it is unlikely that sea otters could feasibly be limited by acute nutritional stress in the two decades since the population decline. Prey overexploitation, an additional cause of acute nutritional stress, can also be ruled out given overall increases in sea urchin abundance at Adak Island during the sea otter decline (Estes et al. 1998). Prey depletion through size selective predation by sea otters would predictably lead to size limited prey populations (Estes and Palmisano 1974, Bodkin et al. 2001, Laidre and Jameson 2006); however, no differences in prey size or biomass were detected between historically used and currently used sites in this study. Although the lack of kelp does affect benthic productivity in urchin barrens (Duggins et al. 1990) and urchin barrens are generally associated with poor nutritional resources (Harrold and Reed 1985), the shift to an urchin dominated system, in itself, was not enough to nutritionally compromise sea otters nor does it explain their current use of restricted habitats. The current and historic use of sea otter foraging locations could also not be attributed to protection from prevailing weather as the majority of currently used sites are fully exposed to prevailing weather. Sea otter foraging locations did, however, differ significantly in terms of their large-scale structural complexity. Currently used locations were characterized by greater variability in seafloor bathymetry, greater percent exposed rock, and more pinnacles per unit area. In contrast, historically used locations were generally broad open coastlines with little bathymetric

relief and little or no exposed rock or coastal structure. The shift to more highly protective habitats is often predator-mediated and can have significant effects on prey habitat use (Stein and Magnuson 1976, Sih 1982). The movement to more protected habitats often entails the increased use of escape terrain (Sih 1980). These findings suggest that the recent shift from historical to current foraging locations by sea otters inhabiting the Bay of Islands was not driven by changes in prey quality or protection from storms but may be attributed to the selective use of escape terrain. It is suggested that the current use of more highly complex habitats is predator-mediated and that post-decline habitat selection is based on predator avoidance.

If killer whale predation is mediating sea otter habitat selection in the Bay of Islands, sea otter prey availability is likely to change over time due to overexploitation (Brown et al. 1999). Intense predation pressure can generate a fundamental trade-off between food and protection, forcing prey species to balance habitat selection between safe and productive locations (Sih 1980, Brown et al. 1999). Sea otters preferentially select the largest and most calorically rich prey first before switching to smaller and less valuable prey (Ostfeld 1982, Garshelis 1983). This association is, however, affected by the ease of access to prey. Depending on prey choices associated with restricted habitats and the mobility of sea otters under the risk of predation, prey depletion and nutritional stress are potential threats to long-term associations with restricted habitats. Areas close to escape terrain are often heavily used for foraging compared to areas located farther away (Pfitsch and Bliss 1985). Since intensive grazing or browsing can greatly reduce plant abundance and quality (Cote et al. 2004, Schoenecker et al. 2004), areas near escape

terrain may be less productive due to grazing stress associated with overharvesting (e.g., depleted plant nutrients and carbohydrate reserves) than farther areas. Although sea otters generally increase the productivity of kelp systems by limiting herbivores, should sea otters continue to be restricted to a limited foraging habitat due to predation pressure from killer whales, further sea otter population declines could result from prey overexploitation and local prey depletion.

This dissertation examined how sea otter resource selection is influenced by habitat complexity and prey quality in two common nearshore habitat types in Alaska, mixed sediment and rocky systems. In the central and western Aleutians, the influence of predator avoidance and the need for protection from storms were additionally investigated as otters in this area are exhibiting use of restricted habitats. Overall, the influence of habitat attributes on sea otter foraging site selection differed between the two study areas, otters inhabiting the heterogeneous benthic system in Kachemak Bay selected rockier habitats over soft sediment habitats whereas otters foraging under the threat of predation in the central and western Aleutians selected habitats with the greatest structural complexity. Although attributes influencing habitat selection differed (e.g., prey availability versus predation pressure), otters in both cases, however, selected more structurally complex habitat. There are several monitoring and management applications for the research findings described in this dissertation. The mapping of nearshore community types in both Kachemak Bay and the central and western Aleutians would enable estimates of the potential sea otter prey in these two nearshore systems. Furthermore, the mapping of community types would enable the monitoring of benthic

community stability over time, a factor important to predicting potential prey resources available to consumers foraging in the nearshore system. When mapped spatially, potential prey energy density, habitat type, and habitat complexity can be utilized as a management tool in sea otter population monitoring in Kachemak Bay and the Aleutians. The availability and extent of both heterogeneous benthic habitats offering different types of prey and habitats suitable for escape terrain in areas where predation is an issue, likely have implications on sea otter population status in coastal Alaska.

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